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Site Index of Scarlet and Black Oak in Relation to Southern Appalachian Soil and Topography

BY
WARREN T. DOOLITTLE

THE STUDY DESCRIBED here is part of an over-all project of soil-site studies of the important commercial species in the Southern Appalachians. In brief, the main project will be an attempt to correlate site indices of the various species growing together on the same land, and then to establish the relationship of significant soil properties and topographic factors to the site index of several of the most important species. After this is done, the site indices of those species not directly studied in relation to the soil can be predicted indirectly through one or more of the several species which have been related to the soil.

In this paper, the results of a study are presented which show a correlation of soil and topography with the site index of scarlet oak (*Quercus coccinea* Muenchh.) and black oak (*Quercus velutina* Lam.).

Description of the Region

Most of the soils in the Southern Appalachians belong to the great soil group known as gray-brown podzolic soils. These typically northern soils develop on the southern mountains where elevation affects the soil-forming processes through low temperatures and a rapid rate of normal erosion. In most of the larger mountain valleys red and yellow podzolic soils are found. These soils have been subjected to higher temperatures and have developed in place for long periods of time. Other minor areas of soil not fitting into either of the two groups above are lithosols and shallow soils, which are found principally in the western part of the region on the plateau areas, but also locally in the mountains on steep slopes, shoulders of mountains, and places where the rock is especially resistant to weathering (e.g., quartzite).

Elevations range from about 1500 feet in some of the valleys to over 6500 feet in the Blue Ridge and Smoky Mountains. Because of this variation in elevation, there is a definite banding or zoning of temperature and rainfall according to elevation. Annual rainfall varies from about 80 inches on the higher mountains at the southern end of the region to less than 40 inches in some of the larger valleys between the Smoky Mountains and the Blue Ridge Mountains. Vegetation is in turn affected by temperature and rainfall; consequently there are many forest types and some 140 native tree species, of which 60 are commercially important (Frothingham, 1931). The most important forest types found in going from lower to higher elevations are yellow pine, yellow pine-hardwoods, oak-hickory, white pine-hardwoods, cove hardwoods, northern hardwoods, and spruce-fir.

Based upon a Ph.D. dissertation under Dr. Harold J. Lutz at Yale University. The author is a research forester at the Southeastern Forest Experiment Station, Forest Service, U. S. Department of Agriculture.

Past Work

Some of the most recent work with soils and site in other parts of the country has revealed the importance of studying certain soil properties and physiographic features.

Carmean (1954), in a study of site and soils in the Douglas-fir region of Washington, found that site index was directly correlated with precipitation and depth to the C horizon, and inversely correlated with gravel content, soil compaction, and elevation. Carmean concluded that site quality is controlled by the amount of available soil moisture supplied to the tree roots during the growing season.

Coile (1948, 1952a and b) and Coile et al. (1953) studied the relation of soils to site index of the southern yellow pines for over twenty years. Coile concluded that soil-moisture, growing space for roots, and aeration for the roots are the most important factors affecting tree growth. He has been very successful in correlating depth of A horizon and imbibitional water values of the B horizon with site index of shortleaf and loblolly pine on well-drained soils.

In southeastern Ohio, Gaiser (1951) was highly successful in correlating white oak site index with aspect, position on slope, and depth of topsoil. Gysel and Arend (1953) studied oak sites in southern Michigan and related mean annual growth to soil characteristics. They found that texture of the subsoil, steepness of slope, and position on slope were the most important characteristics related to growth.

Einspahr and McComb (1951) concluded that topographic position, aspect, depth of soil to bedrock, and percent of slope were the most important factors affecting growth of oak trees in northeastern Iowa. Arend and Julander (1948) studied the relation of soils to oak sites in the Arkansas Ozarks. Their results show site index varying with type of parent material, depth of soil to unconsolidated parent materials, topographic position, and aspect.

In South Carolina, Copeland and McAlpine (1955) studied the relationship of littleleaf disease, site index, soil, and vegetation. In brief, they found site index to be correlated with internal drainage of the subsoil and with the difference between the imbibitional water values of the A and B horizons. From the 13 variables tested for site index, Copeland and McAlpine found internal drainage and erosion highly correlated with the incidence of littleleaf

In Finland, Viro (1947) studied the soil for the effect of loose rock on forest yield. On glacial moraine soils, he found that rock volumes of less than 30 percent did not affect yield. For soils with a rock content of 30 to 60 percent the yield was decreased by 25 percent and a rock content of over 60 percent caused a 50-percent reduction in yield.

Minckler (1941) made a study of planting sites in the Appalachian Valley of Tennessee. He reported that depth of A horizon and consistency of the B horizon were the most important factors to consider in choosing planting sites. He also included aspect and slope as factors for certain species, although these factors are often reflected by soil properties. Auten (1945), in a study of yellow-poplar site quality in the north central states, is in close agreement with Coile as to which soil factors are generally related to site index on well-drained soils. Auten found that the depth of A horizon, depth of soil to a tight subsoil, and topography were closely associated with site index of yellow-poplar.

Humus types may also be of value in soil-site studies. Recently, Hoover and Lunt (1952) published a key for the classification of forest humus types. They recognize eight classes of mull humus layers and seven classes of mors. Their system applies only to well-drained soils. An interesting feature of the system is the fact that depth of A_1 horizon (mineral soil) is included as an added refinement in describing mulls.

Study Procedure

Scarlet and black oak are among the most intolerant of the oak species. By using only

TABLE 1. Distribution of plots by age and site index for scarlet and black oak

Age class (years)	Site index class						
	35–44	45–54	55–64	65–74	75–84	85–94	Totals
	Number of plots						
20–29			1				1
30–39		1	4	1		4	10
40–49	1		3		2	1	7
50–59	1		4	7	4	2	18
60–69	3	11	12	5	5	2	38
70–79	1	5	2	6	3	1	18
80–89		2	3	5			10
90–99		3	1	3			7
100–109							
110–119		1					1
Totals	6	23	30	27	14	10	110

even-aged stands of these species in site index determinations, most of the troubles associated with suppression were avoided. In the Southern Appalachians scarlet and black oak occupy average to below average sites on well-drained upland soils up to 4000 feet in elevation.

Total ages and heights of 4 to 6 dominant and codominant scarlet or black oak trees were determined on each of 110 fifth-acre plots on the Bent Creek Experimental Forest near Asheville, North Carolina. Site indices were computed from Schnur's (1937) site curves (50-year age base) for mixed oak. The only precaution exercised in respect to age was in attempting to confine sampling to stands between 30 and 100 years of age. Table 1 shows that this was done on all except two plots. In Table 2 is shown the number of parent materials and soil series covered in this study as well as the number of plots and average site index for each series.

After the plots had been established and site indices determined for each plot, physiographic and soil measurements were taken. Aspect was measured in degrees azimuth, elevation was measured in feet, position on slope was expressed as a percent of the distance from bottom of the slope to top, and steepness of slope was measured in degrees. Shape of contour was measured with a compass in degrees concave or convex, and shape of slope was measured with an Abney level in degrees concave or convex.

At each plot a 5-foot soil tube was used to sample depth of A horizon, depth of mottling, depth to B_2 horizon, thickness of B horizon, and depth to bedrock. All of these measurements were repeated five times on each plot, except thickness of B horizon and depth to bedrock, which were measured only twice per plot. Depending on the variation in the soil as shown by the tube samples, one or two holes were opened with a post-hole digger on each plot. Samples of the A horizon and B_2 horizon were collected from the holes for laboratory tests. The percent of loose rock (over 3 inches), by volume, was estimated for both the A and B horizons, the humus layer was examined, thicknesses of the various layers determined, and humus type identified according to Hoover and Lunt's (1952) classification.

In the laboratory the soils were air dried, rolled to break down clods, and passed through a 2-mm. sieve. The volume of gravel (2 mm. to 3 inches) which did not pass through the sieve was determined, and a mechanical analysis was made for

TABLE 2. Distribution of plots and site index of scarlet and black oak by parent materials, topography, and soil series

Parent material	Topography	Soil series	No. of plots	Average site index
Light-colored schist, gneiss, and granite (acidic and low mica content)	Valley and intermountain	Hayesville	38	61.7
		Halewood	25	66.7
		Balfour	9	74.2
	High mountain	Porters	16	59.2
		Ashe	4	44.0
Dark-colored, basic rocks (gabbro, diorite, gneiss, etc.)	Intermountain and high mountain	Rabun	3	64.3
Light-colored schist, gneiss, and granite (very highly micaceous)	Valley and intermountain	Watauga	1	49.0
	Intermountain and high mountain	Fannin	7	65.9
	High mountain	Talladega	2	55.5
Colluvial position in respect to any parent materials mentioned above	Footslopes of high mountain and intermountain	Tusquitee	5	79.2
Total and average			110	63.8

both the A and B_2 horizons using the Bouyoucos (1936) hydrometer method. Textural grades were determined according to the International Size Classification, except that only total sand was determined instead of both coarse sand and fine sand (sand = 2.0 to .02 mm., silt = .02 to .002 mm., and clay = <.002 mm.).

Moisture equivalent and imbibitional water values of the B_2 horizon were obtained by the usual procedures, following Briggs and McLane (1907), Fisher (1924), and Coile (1948).

Analysis and Results

A regression analysis showed that there was no significant difference between the site indices for scarlet and black oak growing on the same plots. Therefore both species were combined in the analyses of the relation of site index to soil and topographic features.

Preliminary Analysis

Twenty properties of the soil and topography were examined in a preliminary analysis. These properties or variables are as follows: depth of A horizon, depth to B_2 horizon, thickness of B horizon, depth to bedrock, position on slope, steepness of slope, shape of slope, shape of contour, aspect, elevation, moisture equivalent of B horizon, imbibitional water value of B horizon, percent of sand in A horizon, percent of sand in B horizon, percent of clay in A horizon, percent of clay in B horizon, volume of gravel in A horizon, volume of gravel in B horizon, volume of loose rock (angular cobbles and boulders) in A horizon, and volume of loose rock in B horizon.

Several combinations of properties and crossproducts were also examined. Each of the 20 variables was separately plotted

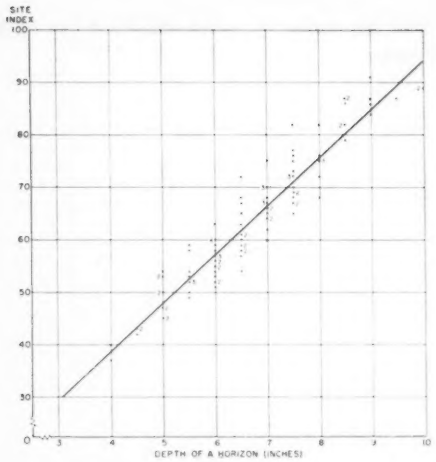

FIGURE 1. *The relation of site index for scarlet and black oak to depth of A horizon. Each dot represents one plot, except where indicated otherwise by an adjacent number.*

over site index. From these graphs it was evident that one of the strongest variables was depth of A horizon (Fig. 1). It also appeared likely that position on slope might be important, although Figure 2 shows the scatter of plots to be greater than for depth of A horizon. Graphs of other variables showed much less relation to site index at this time (e.g., see Fig. 3).

The next step was to develop a regression equation containing the strongest independent variable, depth of A horizon:

$$Y = b_0 + b_1X_1$$

Here, Y is site index and X_1 is depth of A horizon. The regression of Y on X_1, in this equation, proved to be highly significant. Residuals from the equation were plotted over all remaining variables. The next strongest variable, so indicated, was added to the equation, and residuals from the new equation were plotted over the remaining variables.

After a series of tests and plottings, it was determined that at least three independent variables belonged in the regression equation. These variables were depth of A horizon (X_1), position on slope (X_2), and percent of sand in A horizon (X_8). From the plotted residuals, it was also determined that five additional variables should be tested further for some possible value to the equation. Final analysis of the eight variables was made by the C-multiplier method.

Final Analysis

Variables included in the computation of C-multipliers were depth of A horizon, position on slope, percent of sand in A horizon, elevation, ratio of silt plus clay to moisture equivalent of B horizon, percent of gravel and loose rock in A horizon, aspect, and the second power of aspect.

It is of interest to note that the residual effects of aspect follow exactly the pattern of the popularly accepted version of the relation of site to aspect. The graph in Figure 4 indicates that the equation $Y = b_0 + b_1X_1 + b_2X_2$ will slightly overestimate site index on the poorer sites (south and west aspects) and slightly underestimate site index on the better sites (north and east aspects). However, the error in estimate would be very minor and becomes even less when percent of sand in A horizon (X_8) is added to the equation. As shown later, aspect does have a larger total effect on site index than is shown by the graphs, but it is confounded primarily with depth of A horizon, and somewhat less with percent of sand in A horizon and position on slope.

Significance tests of the eight regression coefficients showed that depth of A horizon (X_1) and percent of sand in A horizon (X_8) were highly significant (1-percent level), and position on slope (X_2) was significant at the 5-percent level. None of the other variables was significant, and the final equation becomes the same as it was before the last tests were made:

$$Y = b_0 + b_1X_1 + b_2X_2 + b_8X_8$$

By substituting numerical values of the b-coefficients the equation becomes:

$$Y = 38.7690 + 8.8057X_1 - 0.0477X_2 - 0.4620X_8$$

An examinaiton of the precision of this equation indicates that 95.74 percent of the total variation is accounted for by these three variables alone. The standard error of the mean site index value (63.76) is ± 2.65 feet for a probability of 2 out of 3 estimates.

Discussion

The growth of a tree is an expression or function of a number of factors, many of which are environmental. The more important factors of the environment are temperature, humidity, rainfall, parent material of the soil, soil profile development, topography, and depth to the water table. Environmental factors act and interact with vegetation, through time, to become expressed best by the soil profile itself. This is observed in the areas where the soil is mature and has developed in place for a long period of time.

In the Southern Appalachians there are a great number of examples of soils which are well developed and which reflect quite fully their environment. On the other hand, there are also a number of young soils on steep mountain slopes which have a rapid rate of normal soil erosion; these soils do not completely represent or reflect all environmental factors.

Since some of the soils in this study are relatively young, it was necessary to examine thoroughly not only the soil, but also

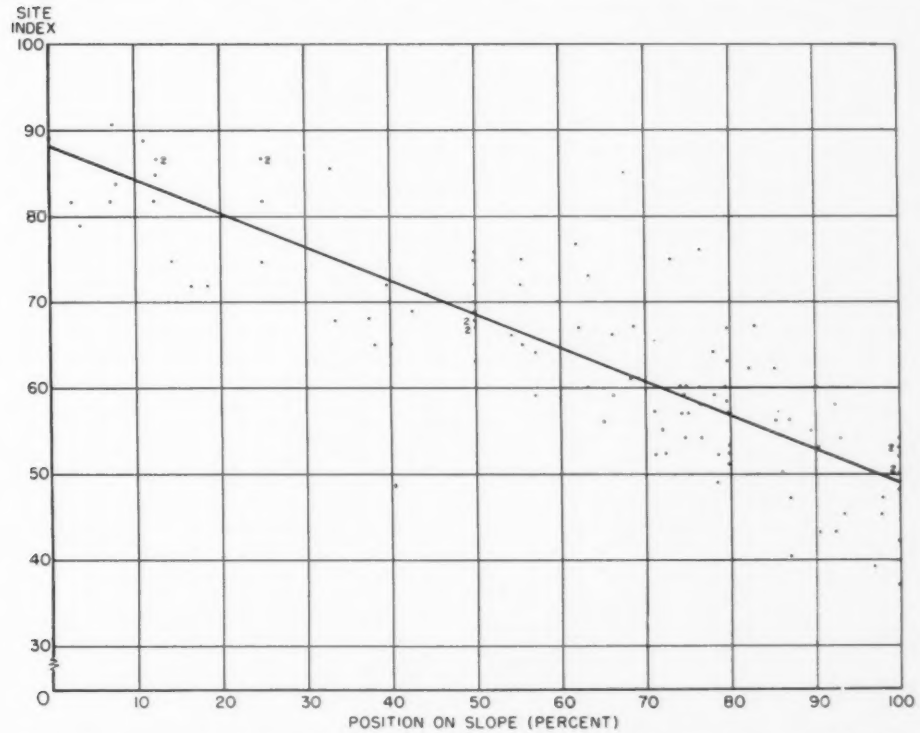

FIGURE 2. *The relation of site index for scarlet and black oak to position on slope. Each dot represents one plot, except where indicated otherwise by an adjacent number. Position on slope is the percent of distance from bottom to top.*

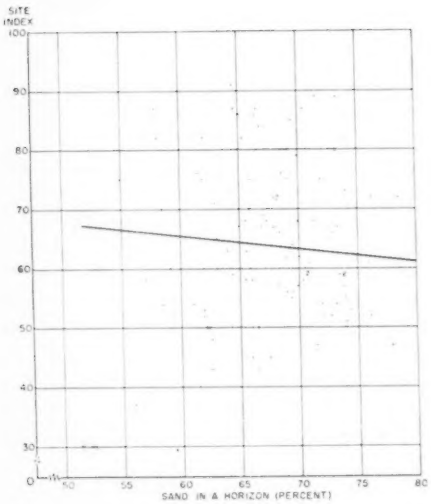

FIGURE 3. *The relation of site index for scarlet and black oak to percent of sand in A horizon. Each dot represents one plot, except where indicated otherwise by an adjacent number.*

topography, in an attempt to correlate recognizable soil and topographic properties with site index. The analysis has shown that depth of A horizon is the best single gauge of site index. This property alone accounts for 90.97 percent of the variation in site index. It is also easily measured, and if the soil has not been abnormally stripped of its A horizon, there is no reason why this property should not be used in predicting site index.

Depth of A horizon appears to be a very sensitive function of many of the other factors of the soil and environment—just as site index is a reflection or function of many of the same factors, including depth of A horizon. Although some of the other soil properties also tend to reflect environment, this was not indicated as strongly in the analysis as it was for depth of A horizon. However, two other properties of the soil and topography do add refinement and precision to the prediction of site index. These properties are percent of sand in A horizon and position on slope. On two soils which have equal depth of A horizon, site index will be lower on the soil having the higher percent of sand. Position on slope adds less precision to the estimate than either of the two properties of the A horizon.

Figure 5 shows how all three variables combine to give an estimate of site index. The range of values for position on slope is 0 (bottom of slope) to 100 percent (top of ridge) and the corresponding range of its effect on site index is from 0 to 4.77 feet. The range of values for sand in A horizon is from 50 to 80 percent with an over-all effect on site index of from 0 to 13.86 feet. Because of the minor contribution of position on slope to the equation, it is possible to show the values of site index in a simple 2-way table (Table 3) for middle slope positions—with a plus 2-foot correction for lower slopes and a minus 2-foot correction for upper slopes.

In Table 4 the distribution shows that northerly and easterly aspects are consistently better sites than southerly and westerly aspects. This is best illustrated near the bottom of the table where only two

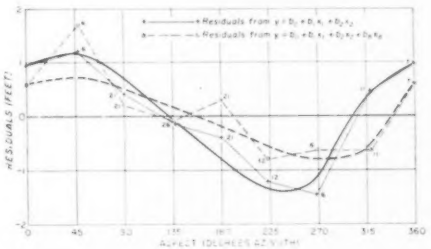

FIGURE 4. *Residuals from the equations* $Y = b_0 + b_1X_1 + b_2X_2$ *and* $Y = b_0 + b_1X_1 + b_2X_2 + b_8X_8$ *as related to aspect. Crosses and circled dots indicate mean values of residuals (see legend) for a given class of aspect.*

TABLE 3. Site index of scarlet and black oak by percent of sand and depth of A horizon for middle slope positions.[1]

Depth of A horizon (inches)	Percent of sand[2] in A horizon			
	80	70	60	50
3	26	30	35	40
3½	30	35	39	44
4	35	39	44	49
4½	39	44	48	53
5	43	48	53	57
5½	48	52	57	62
6	52	57	61	66
6½	57	61	66	71
7	61	66	70	75
7½	65	70	75	79
8	70	74	79	84
8½	74	79	84	88
9	79	83	88	93
9½	83	88	92	97
10	87	92	97	101

[1]For lower slopes, add 2 feet to site index values; for upper slopes, subtract 2 feet from site index values.
[2]Percent of sand by the International Size Classification (0.02 to 2.0 mm.).

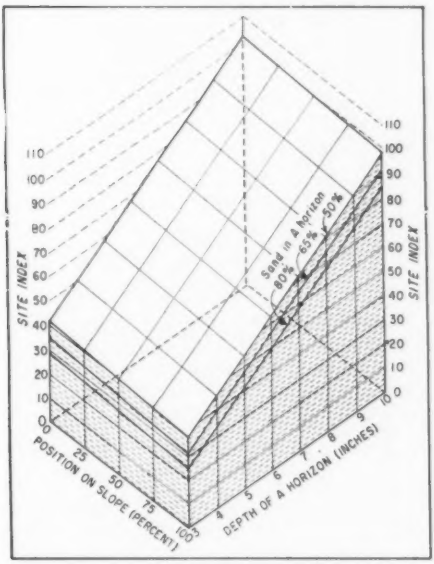

FIGURE 5. *Block diagram for site index of scarlet and black oak as related to depth of A horizon, position on slope, and sand in A horizon.*

aspect groups are listed. The information in this table shows that, alone, aspect does have a definite effect on site index—as is popularly believed. However, in the analysis of data, aspect was found to be distinctly nonsignificant. This is due mainly to the confounding of aspect with other variables such as depth of A horizon.

The other variables tested in this study proved unimportant, and will not be discussed individually. It is likely that for certain narrow classes of soils or topographic locations some of these variables would also be important in their contribution to an estimate of site index.

It is also possible that not all the important properties of the soil were considered in this study. Certain of the factors omitted in this work, although perhaps of importance, are very difficult to measure, and hence could not readily be used in determinations of site quality. This applies particularly to conditions at the deeper rooting levels.

In the Southern Appalachians the soils are generally quite friable and somewhat sandy. Laboratory tests show imbibitional

TABLE 4. Site indices of scarlet and black oak by aspect.

Aspect	Number of plots	Average site index
N	5	63.1
NE	12	70.9
E	15	66.4
SE	22	67.5
S	33	61.2
SW	16	58.9
W	5	57.0
NW	2	62.5
N and NE	17	68.6
E and SE	37	67.1
S and SW	49	60.4
W and NW	7	58.6
N, NE, E, and SE	54	67.5
S, SW, W, and NW	56	60.2
Total and average	110	63.8

water values ranging from 3.71 to 9.47 for the B_2 horizon, which indicates that all of the soils in this study are considered friable, according to Coile's (1948) range of values for Piedmont soils. This comparison also seems to indicate that there should be no layers of soil or soil material in this study which would prevent tree roots from penetrating to considerable depths. If this is true, tree roots may reach variable quantities of ground water depending on whether the water table is within reach, and, if it is within reach, whether the water table is temporary (i.e., perched from the winter season) or permanent (as it may be near the bottoms of slopes or along drainageways).

Tree roots do penetrate Southern Appalachian soils to great depths. Unpublished studies at the Coweeta Hydrologic Laboratory, near Franklin, North Carolina, show that roots of small trees can be traced to depths of over 8 feet, and roots of large trees can be traced to even greater depths. The soils and geology at Coweeta are quite similar to those at Bent Creek, and the same principles should generally apply in both places.

In the study at Bent Creek, measurements of soil and bedrock were limited to a depth of 60 inches. Therefore, any effect on site index contributed by factors such as soil, water table, or bedrock below this depth cannot be stated here. These effects could not readily be utilized in site-index measurements anyway.

A final relationship examined in this study was that between humus types and site index. A wide range of humus types was encountered, but the bulk of them fell into the class of duff mulls (Table 5). Mor humus types had a tendency to occur on the drier sites and under ericaceous shrubs, such as laurel and rhododendron. Rhododendron usually grows only on the moist sites and, since scarlet and black oak tend to grow on drier sites, most of the mors found in this study were on very dry sites and under laurel bushes. Thus, the site indices of these plots were low, whereas if the study areas had included more rhododendron or similar species, a larger proportion of the plots would have shown some mors on good sites too.

Generally, site index increases as the A_1 horizon increases in depth. In other words, a rather uniform increase in site index takes place with the change from mor through duff mull to true mull humus types. This relation is illustrated in the following tabulation, which is a summary of Table 5:

Humus type	*Depth of* A_1	*Average site index*
Mors	None	49.8
Duff mull	Shallow	58.2
Duff mull	Deep	65.9
Mull	Deep	74.0
Mull	Very deep	87.4

It appears, then, that for the scarlet and black oak types, the humus type is a fairly good indicator of site quality. It should also be recognized, however, that in certain situations the presence of ericaceous species, especially rhododendron, may lead to the formation of mors even though the site quality is high.

TABLE 5. Humus types in relation to site index of scarlet and black oak.

Humus type[1]	Number of plots	Range of site index	Average site index
Mors			
Thick felty	6	37–54	47.8
Thin felty	18	39–59	50.5
Total and average	24		49.8
Duff mulls			
Thick (shallow A_1)	3	59–64	61.3
Thick (deep A_1)	3	43–60	49.3
Thin (shallow A_1)	26	45–67	57.8
Thin (deep A_1)	21	57–79	68.3
Total and average	53		61.7
Mulls			
Coarse (deep A_1)	5	62–76	66.5
Coarse (very deep A_1)	3	87–91	89.0
Medium (deep A_1)	20	67–87	75.8
Medium (very deep A_1)	5	84–89	86.4
Total and average	33		77.2
Grand total and average	110		63.8

[1]See Hoover and Lunt (1952).

Summary and Conclusions

The purpose of this study was to correlate soil and topography of the Southern Appalachians with site index of scarlet and black oak.

Accordingly, site index and 20 properties of the soil and topography were examined on 110 plots on the Bent Creek Experimental Forest. By regression analysis it was determined that only three of the 20 properties were of significant value in predicting site index. The three properties are depth of A horizon in inches, position on slope in percent of distance from bottom to top of the slope, and percent of sand in A horizon. The best expression of the estimate of site index is in the equation:

$$Y = b_0 + b_1X_1 + b_2X_2 + b_3X_3$$

Site index = 38.7690 + 8.8057 (depth of A horizon, inches) − 0.0477 (position on slope, percent) − 0.4620 (sand in A horizon, percent)

The standard error of the mean site index value (63.76) is ± 2.65 feet.

Although properties such as aspect have definite effects on site index, they are almost completely accounted for by one or all of the three properties already in the equation.

An examination of humus types revealed that they are fairly good indicators of site quality on scarlet and black oak sites. Mor humus types usually occurred on the poorest dry sites, duff mulls on intermediate sites, and true mulls on the best moist sites. It was also found that mors were often closely associated with ericaceous vegetation (laurel in particular).

A number of soil factors were not examined because they are not readily measurable. One of the best examples is depth to water table, which is extremely variable in the mountains and may have considerable effect on site quality. However, most of these factors, including depth to water table, are probably accounted for by depth of A horizon and other measurable properties of the soil.

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Pathological Deterioration of Looper-Killed Western Hemlock on Southern Vancouver Island

BY
N. T. ENGELHARDT

DURING 1944-46 an outbreak of the western hemlock looper (*Lambdina fiscellaria lugubrosa* (Hulst)) occurred on southern Vancouver Island. As a result of this infestation, 50 thousand acres of mature and overmature western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), and amabilis fir (*Abies amabilis* (Dougl.) Forbes) were severely defoliated. Most of this damage was concentrated in the valleys of the Klanawa, Caycuse, Sarita, and Nitinat Rivers, which drain the western slopes of Vancouver Island between Cowichan Lake and the Alberni Canal (Fig. 1). Within the defoliated areas complete mortality occurred on some 15 thousand acres containing approximately 500 million board feet of timber (Kinghorn, 1954).

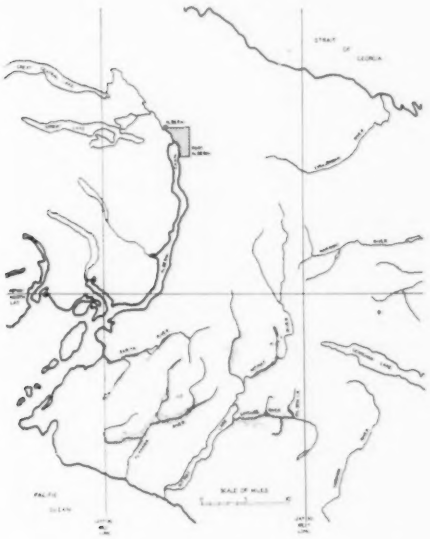

FIGURE 1. *Map of portion of southern Vancouver Island, B. C. Hatching represents areas of hemlock and associated species killed by the hemlock looper during the 1945-1946 outbreak.*

One of the important considerations facing the forest industry following the looper attack was that of determining the maximum period during which the economic salvage of killed stands would remain feasible.

Although studies of the deterioration of western hemlock had been undertaken previously in the Pacific Northwest region

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FIGURE 2. *Typical stand of western hemlock in the Wilson Creek area, seven years after attack by the hemlock looper.*

(Boyce, 1929; Buchanan and Englerth, 1940; Kimmey and Furniss, 1943; Childs and Clark, 1953), none provided information specific to insect-killed stands. Since it was appreciated that cause of death could influence the nature and rate of deterioration (Riley and Skolko, 1942) and since future outbreaks can be anticipated, it was considered of value to initiate studies in the affected areas.

This report summarizes the results of studies carried out in three severely affected areas on southern Vancouver Island.

Methods

In view of the sampling problems encountered, it was necessary to carry out examinations in felled and bucked timber made available through salvage operations then in progress. Three examinations were made. The first field examination was carried out in the valley of the Sarita River in 1948. Trees examined in this area were located within a strip one-quarter mile long by 100 ft. wide. The second examination was carried out in 1950 on 13 one-fifth-acre plots established in the valley of the Klanawa River. The final examination was made in 1953 on a one-acre plot established in the valley of Wilson Creek (Fig. 2). These areas, although selected because of their similarity in stand composition, site quality, and age distribution, were considered to be representative not only of the affected stands but also of the hemlock type common to the region as a whole. Hemlock comprised approximately 80 percent of the total stand volume. Site indices of hemlock ranged from 110 to 120 and average stand ages from 200 to 230 years. In each of these areas 95 percent or more of the hemlock had been killed.

Information on the year of death of trees which exhibited varying degrees of defoliation was gained by cooperators[1] through the examination of permanent sample plots established in areas of severe attack. These examinations were discontinued in 1950 when most of the plot trees were felled during the course of salvage operations. Since arrangements could not be completed to section representative trees on a sufficient number of the permanent sample plots prior to 1950 or on any of those remaining after this date, it was necessary to employ an arbitrary time scale on which to evaluate the rate of deterioration. The basis employed was the year of collapse of the looper outbreak, namely, 1946. Studies have shown (Kinghorn, 1954) that few hemlock completely defoliated in 1944, 1945, and 1946 recovered, and since living trees were excluded from the deterioration analyses, 1946 may be interpreted not only as the year of death but also as the commencement date for the evaluation of stand deterioration. Thus, conditions encountered in 1948, 1950, and 1953 were considered to represent the cumulative deterioration 2, 4, and 7 years after cessation of the outbreak.

Mensurational data[2] were obtained for all hemlock felled for detailed analysis in the sample areas. All trees 12 in. and over at d.b.h. were scaled in accordance with current standards of utilization (Province of British Columbia, 1944). In addition, the location and extent of all breaks, splits, and shatter were noted.

Measurements of radial penetration of decay were obtained by chopping into the logs at intervals of 10 ft. from stump to a 10-in. top. At each point of examination the average depths of incipient and advanced decay were measured and their characteristics described. Decays were identified in the field by means of sporophores associated with them. In the absence of sporophores, wood samples containing the incipient stage of the unknown decay were collected for subsequent cultural identification.

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[1]Personnel of Forest Zoology Unit, Forest Biology Laboratory, Victoria, B. C.

[2]Mensurational data included species, diameter breast height (d.b.h.) outside bark, total height, bark thickness, stump height and diameter, age and increment, and log length.

All volumes were computed in board feet according to the British Columbia Log Scale (Province of British Columbia, 1944), and in accordance with standard culling procedures (Province of British Columbia, 1942), with the exception that decay volumes were deducted prior to those for breakage. Gross merchantable volume was measured as the volume between stump height and a 10-in. top. The entire volumes of broken or defective logs under 16 ft. in length were culled for decay and breakage. Logs 16 ft. or over were culled if at least one-third of their gross volume in sound wood could not be recovered after deductions for decay. Trees were culled if 50 percent of their gross volume could not be recovered in sound wood.

Deterioration volumes were computed by reducing the diameter of the logs according to the visible extent of radial penetration by decay fungi. In computing the average depth of radial penetration, the depth of decay at each 10-ft. interval along the merchantable bole from stump height was taken to represent the average depth of decay five feet above and below the point of measurement. To determine the average depth of decay for the entire bole, the depths of decay measured at each 5-ft. section were summed and divided by the total number of sections. The same procedure was followed in computing the average radius of decay in individual logs.

Heart-rot volumes were assigned from average values computed for living hemlock in adjacent areas by Buckland *et al.* (1949). These values, which were derived following extensive sampling, were considered to be more representative of the average volume of heart-rot applicable to western hemlock in the region than values obtained during the limited sampling of the present study.

Results

Losses associated with decay and breakage. Average total losses attributed to decay and breakage increased progressively from year of death (Table 1 and Fig. 3). By the seventh year, all dead trees had reached the stage of absolute or arbitrary cull. The most important source of loss was that caused by sap-rot which entered the trees following death. Losses from breakage

TABLE 1. Losses sustained in looper-killed hemlock on southern Vancouver Island

Number of years of deterioration	Sap-rot losses	Breakage losses	Total losses[1]
	percent	*percent*	*percent*
2	19	3	46
4	36	6	66
7	67	9	100

[1]Total losses include average heart-rot losses of 24% as computed by Buckland *et al.* (1949).

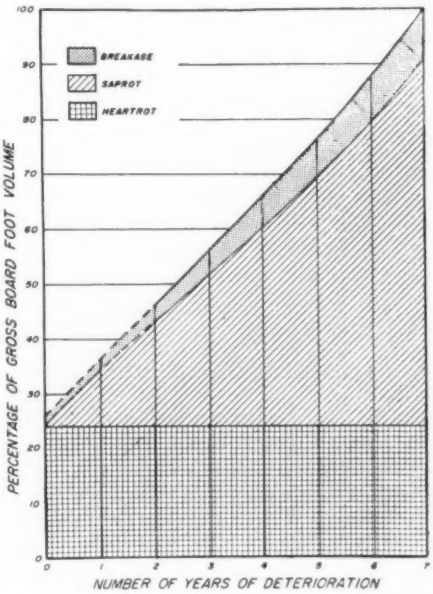


FIGURE 3. *Total losses from decay and breakage in looper-killed hemlock.*

were considerably lower. Most breakage, moreover, was attributed to the large volumes of both sap-rot and heart-rot present at the time of felling (Figs. 4, 5, 6, and 7). Losses attributable to heart-rots present in the trees prior to their death were included in the computation of total losses. Twenty-four percent of the gross volume was deducted for heart-rot in each year of examination. Although no significant increase in volume was apparent, it should not be concluded that the activity of heart-rot fungi ceased following the death of the trees. It is more likely that the sampling techniques employed were inadequate in regard to determination of the small increase likely to occur during the period of study.

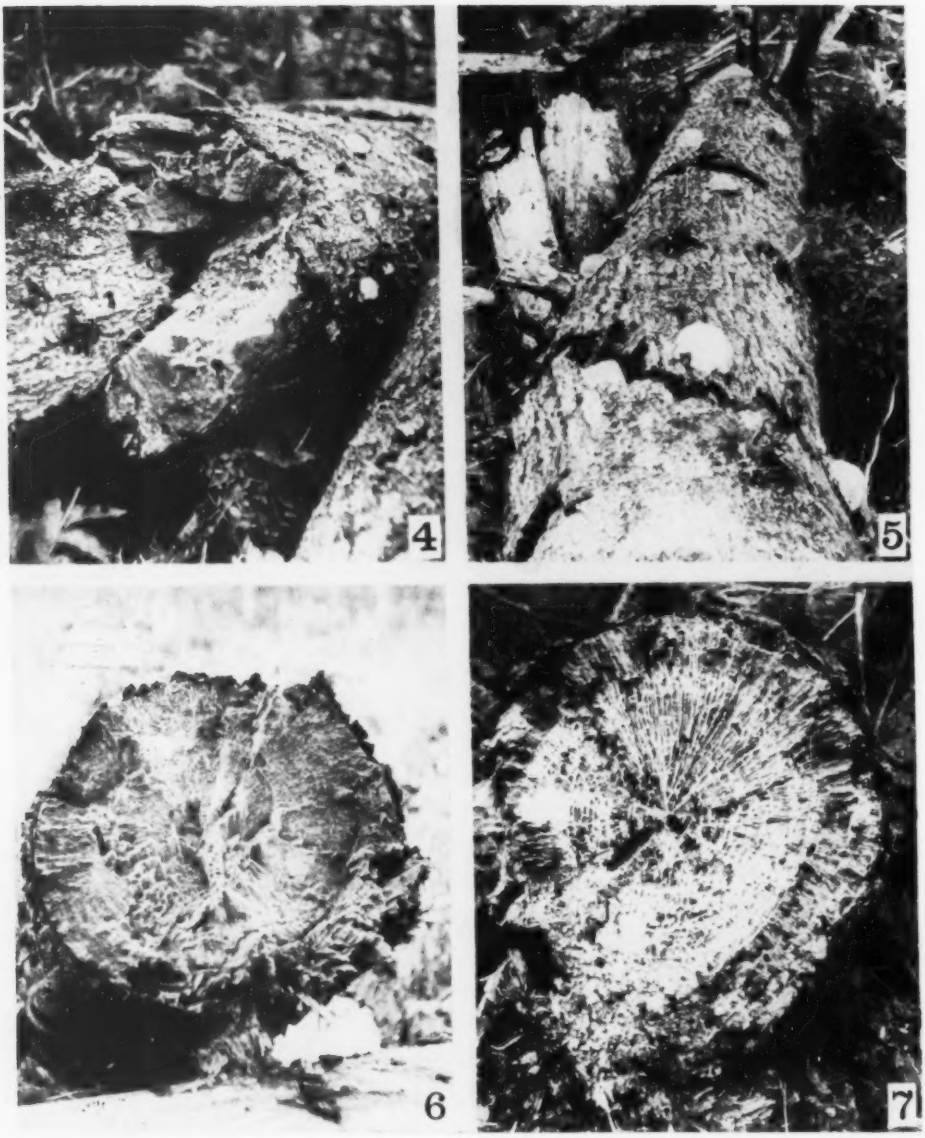
Analyses showed (Table 2) that the average depth of radial penetration increased with time from year of death and that the average depth of radial penetration did not vary significantly with d.b.h. In view of these findings it is to be expected that volumetric losses, expressed in relation to the gross merchantable volume, would decrease with increase in diameter. Figure 8 demonstrates the average reduction in gross volume which may be expected to occur as a result of sap-rot penetration. Figure 8 was derived from curved gross volume data (Province of British Columbia, 1947) for site 120, reduced according to the average radial penetration computed after 2, 4, and 7 years of deterioration. Curved gross volumes were used for this purpose rather than those computed in this study because the latter were found to fluctuate unduly. These fluctuations were attributed to inadequate sample size and, to a lesser extent, to differences in site. It should be mentioned that these data have reference only to losses sustained from sap-rot and that no arbitrary culling standards were adopted in their determination. Thus, although it is indicated in Fig. 8 that 20-in. trees do not reach absolute cull until the seventh year of deterioration, the addition of heart-rot to this size class would demonstrate that the termination of the period of economic salvage, assumed to be at the point of 60 percent loss, would be reached within four years. Similarly, economic salvage of the 30-in. d.b.h. class would not be possible after five years and of the 40- and 50-in. classes not after six years.

TABLE 2. Radial penetration of sap-rot in hemlock in relation to tree size

Diameter class (inches)	Number of years of deterioration		
	2	4	7
	Radial penetration in inches		
10	....	1.5	2.8
15	0.9	1.4	5.4
20	0.5	1.6	4.5
25	0.8	2.6	5.1
30	1.3	2.7	5.3
35	1.1	2.5	5.6
40	1.3	2.8	5.4
45	1.6	2.1	7.6
50	....	1.3	5.9
55	0.4	2.8	....
60	1.0	....	....
Average depth of penetration	1.0	2.4	5.7
Computed value of t	1.881	1.896	2.235
Table value of $t(.01)$	2.669	2.868	2.845

Basis: 258 trees.

When the trees were analyzed on a log basis, it was found that the average losses caused by sap-rots increased with increasing height above ground (Table 3). This trend was found to be in direct contrast to that reported by Riley (1940) in his study of bark-beetle-killed spruce on Gaspé Peninsula in Quebec. Although the limitations of this study did not permit investigating the reasons for this trend, it is believed that the moisture content present in the lower portions of the trees was too high to allow vigorous growth of the wood-rotting fungi. Also, the smaller percentage of sapwood present in the lower portions of the boles may have further re-



FIGURES 4, 5, 6 and 7. *Typical breaks occurring in hemlock during felling. Note numerous sporophores of* Fomes pinicola *(Sw.) Cooke in Figure 5 and deep penetration of decay in Figures 6 and 7.*

TABLE 3. Relation of volume of sap-rot to position of logs in tree (curved values)

Number of years of deterioration	Percentage of gross volume lost through sap-rot							
	First log		Second log		Third log		Fourth log	
	Average length ft.	Sap-rot %	Average length ft.	Sap-rot %	Average length ft.	Sap-rot %	Average length ft.	Sap-rot %
2	38	10	35	25	27	49	22	75
4	34	21	30	52	20	85	16	100
7	34	58	20	91	18	97	21	100

stricted fungal activity. These results do demonstrate again, however, that smaller diameter logs are subject to heavier volume losses than those of larger diameter for equal sap-rot penetration.

As would be expected, the rapid inroads made by the wood-rotting fungi, together with a proportionate increase in breakage, had a decided effect on the length and number of merchantable logs recovered from the killed trees. Log length decreased steadily as the deterioration advanced, irrespective of the portion of the bole from which the log was taken. The first three logs cut from the tree of average diameter in the second year, for example, were 38, 35, and 27 ft. in length, respectively, while those cut from the same relative positions in the seventh year were only 35, 20, and 18 ft. in length, respectively. Since the percentage of decay not only increased with height above ground, but also with the length of the deterioration period, the number of merchantable logs recovered rapidly decreased from five in the second year to one in the seventh.

Although logs under 16 ft. in length were arbitrarily culled for decay or breakage, it was considered of interest to determine what percentage of the total gross merchantable volume of the stands was associated with this size of log and, also, to determine whether the percentage of defect present was higher than that found in logs of merchantable size. Subsequent analyses indicated that total losses from this source remained low, averaging less than 10 percent of the gross merchantable volume of the trees examined. The percentage of their gross volume associated with decay, however, was much higher than that encountered in merchantable-size logs. At the end of the fourth year of deterioration, for example, decay losses

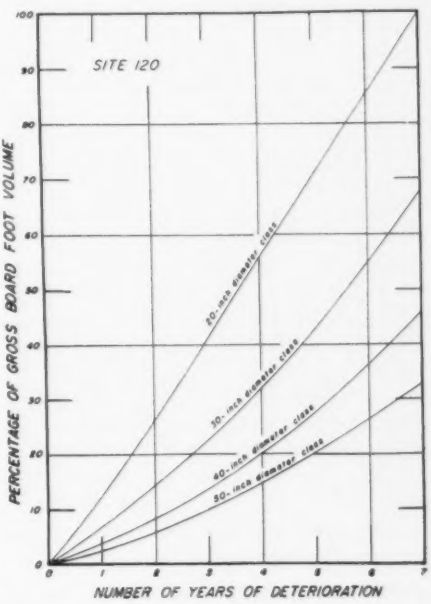


FIGURE 8. *Percentage of gross board foot volume lost through deterioration due to sap-rot penetration.*

amounted to 31 percent in logs over 16 ft. and 73 percent in those under 16 ft. It is apparent from the values given in the example, and from those derived for other years of analysis, that the presence of proportionately higher volumes of decay will increase the number of logs of unmerchantable size occurring in trees at the time of felling.

Entrance courts for deterioration fungi. The more important avenues through which deterioration fungi were considered to gain entrance were insect holes, broken tops, bark cracks, branch stubs, scars, and roots. Bark- and sapwood-mining insect entrance and exit holes appeared to be of particular importance during the early stages of deterioration. Thus, not only was there a higher percentage of infection in those portions of the bole where insect holes were most numerous, but also it was found that the frequency of deep-seated infections was higher at these points.

As deterioration progressed, breakage in the tops and branches increased, bark cracks developed, and bark began to pull away from the sapwood around branch stubs and scars, thus providing many more avenues of entrance for decay fungi. By the fourth year of deterioration the zone of fungal activity had spread out from the infection points and coalesced to form a solid but irregular ring of decay around the periphery, as well as over the entire length of the tree. Many of the fungi found attacking the first six feet of the bole appeared to gain entrance at or below ground level. Decay caused by these fungi was, in nearly all cases, far more advanced at ground level than at stump height.

Fungi causing decay. Ten fungi were found to contribute to deterioration (Tables 4 and 5). *Fomes pinicola* (Sw.) Cooke was by far the most important wood-rotting fungus with respect to number of infections and percentage of total decay. This fungus was responsible for the only brown cubical rot identified during the study. All the remaining identified and most of the unidentified decays were caused by white-rotting fungi.

Fomes pinicola caused 56 percent of the total infections and 81 percent of the total decay. The percentage of total decay attributed to this fungus was found to be consistently high in all years. It is of interest to note that *Fomes pinicola* has been reported by Boyce (1929) and Buchanan (1940) to be responsible for most of the losses from decay in wind-thrown hemlock in Washington and Oregon. It would appear, therefore, that this fungus is probably the most important cause of decay in dead hemlock in the Pacific Northwest.

The number of infections and amount of decay associated with identified white-rotting fungi were relatively insignificant when compared to those of *Fomes pinicola*. In no case was more than 9 percent of the total infections, or more than 2.7 percent of the total decay volume, associated with any of these rots. In terms of volume infected, the more important white rots were those caused by *Fomes annosus* (Fries) Cooke, *Ganoderma applanatum* (Pers.) Pat., and *Polyporus abietinus* Dicks. ex Fries, which accounted for 2.7, 2.2, and 2.1 percent of the total decay volume, respectively. In terms of percentage of total number of infections, however, the most important rots were *P. abietinus*, *Armillaria mellea* (Vahl ex Fries) Quél., *Ganoderma applanatum*, and *Fomes annosus*, which were associated with 9, 8, 4, and 3.6 percent, of the infections, respectively.

Only three of the white-rotting fungi, *Ganoderma applanatum*, *Fomes annosus*, and *Ganoderma oregonense* Murr., were consistently isolated in all three years of analysis. *Amillaria mellea* was isolated in the last year of analysis only, although there was evidence of its presence in the stumps of trees examined in the earlier analyses. *Polyporus abietinus*, which appeared to attack only the sapwood, was isolated only in the first two years. Some

TABLE 4. Fungi associated with the deterioration of looper-killed hemlock

Fungus	Type of rot	Total number of infections
Fomes pinicola (Sw.) Cooke	Brown cubical	230
Polyporus abietinus Dicks. ex Fries	White pocket	37
Armillaria mellea (Vahl ex Fries) Quél.	White soft	33
Ganoderma applanatum (Pers.) Pat.	White mottled	18
Fomes annosus (Fries) Cooke	White pocket	15
Ganoderma oregonense Murr.	White spongy	10
Poria tsugina (Murr.) Sacc. and Trott.	White pitted	4
Polyporus resinosus Schrad. ex Fries	White stringy	2
Polyporus circinatus Fries	White pocket	1
Polyporus circinatus var. *dualis* Pk.	White pocket	1
Unknown	White	62
Total		413

old fruiting bodies of this fungus were noted in the final year of analysis but no significant amount of decay was recorded.

During the first two years of deterioration, *P. abietinus* infections were apparently confined to the basal log but by the fourth year it was found to have infected the upper bole as well. With the exception of

TABLE 5. The relative importance of fungi associated with the deterioration of looper-killed hemlock

Fungus	1948 analysis		1950 analysis		1953 analysis	
	Percentage of total number of infections	Percentage of total decay volume	Percentage of total number of infections	Percentage of total decay volume	Percentage of total number of infections	Percentage of total decay volume
Fomes pinicola	62.2	64.4	56.2	82.9	47.0	86.1
Polyporus abietinus	1.4	0.2	22.9	5.7	---	---
Armillaria mellea	---	---	---	---	28.2	2.6
Ganoderma applanatum	1.4	1.8	2.6	0.7	10.3	3.4
Fomes annosus	4.2	2.2	3.3	2.5	3.4	3.0
Ganoderma oregonense	2.8	0.5	0.7	0.2	4.3	1.8
Poria tsugina	2.8	3.0	---	---	---	---
Polyporus resinosus	---	---	0.7	Trace[1]	0.8	0.4
Polyporus circinatus	---	---	0.6	0.5	---	---
Polyporus circinatus var. *dualis*	---	---	0.6	0.1	---	---
Unknown	25.2	27.9	12.4	7.4	6.0	2.7
Totals	100.0	100.0	100.0	100.0	100.0	100.0

[1]Less than one-tenth of one percent.

Armillaria mellea, which attacked the butt end of the basal log only, all other fungi isolated, including *Fomes pinicola*, were found to attack all sections of the bole indiscriminately. In this regard, *Fomes annosus*, whcih is generally considered to cause a root and butt rot, was frequently isolated at heights well above the basal log, with no apparent association with basal infections, although the latter were frequently present in the same trees.

Several other fungi were isolated in culture but none was found to be associated with deductible volumes of decay. These fungi were, in order of their frequency of occurrence, *Trechispora brinkmanni* (Bres.,) Rog. and Jacks., *Stereum sanguinolentum* Alb. and Schw. ex Fries, *Stereum chailletii* Pers., *Fomes pini* (Thore) Lloyd, and *Omphalia campanella* Fries.

Fruiting bodies of *Fomes pinicola* occurred with relative abundance on standing trees, often over their entire length. Sporophores usually developed in bark crevices (Fig. 4) or on the underside of branch stubs. Most, however, did not appear until the decay reached an advanced stage. Sporophores of other decay fungi were relatively scarce with the exception of those of *Polyporus abietinus*, which developed in profusion in bark crevices during the early stages of deterioration.

Discussion and Summary

The long-term nature of the study, together with the need for sampling stands within the sphere of salvage operations, necessitated locating sample plots in three separate areas. Although minor differences in stand conditions were encountered in each sample area, they were not considered of importance in respect to the general deterioration of stands. As the stands sampled were considered to be representative of the hemlock type on the west coast of Vancouver Island, it is believed that the data obtained may be related to future outbreaks of a similar nature in the same region.

On the basis of the samples obtained, deterioration of the killed stands progressed rapidly. The principal agents responsible for this rapid deterioration were wood-rotting fungi which entered the trees shortly after their death. Some deterioration was also caused by secondary insects but since this damage was limited primarily to degrade of the sapwood, losses from this source were not considered separately from those caused by sap-rot. Although some breakage, caused by weathering and decay activity, occurred prior to felling, most of the losses attributed to this source took place during felling and, as such, were considered a result of rather than a cause of deterioration. Nevertheless, since breakage is unavoidable in felling deteriorated timber, losses from this source were included whenever total loss volumes were computed. As an average depth of about one inch is normally lost through slabbing in a sawmill, actual losses in sawlog material, from decay alone, would be considerably lower for the first two years of deterioration than that indicated in the computations.

In the early stages of deterioration most fungi attacked the sapwood in a sporadic fashion forming numerous scattered pockets of decay. As deterioration advanced, these pockets coalesced to form an irregular ring of decay. All sap-rot deductions, therefore, were computed on the basis that a solid ring of decay developed around the periphery of the logs. In the first two years following death, most decay was in the incipient stage, and apart from the uppermost logs, did not penetrate on the average more than one inch radially. Beyond the second year of deterioration, radial penetration by decay fungi increased rapidly and, as a result, the sawlog volume was generally reduced below the point of economic recovery by the fifth year, with only small volumes of relatively low quality sound wood remaining in the basal logs of the larger trees.

It is generally accepted that most decay fungi gain entrance to living trees through broken tops, scars, roots, and branch stubs.

As evidenced by this study, however, it would appear that other means are utilized by decay fungi in reaching the sapwood of dead trees, particularly in the early stages of deterioration. Thus, insect holes appeared to be an avenue of entrance for decay fungi. Although supporting evidence was primarily observational, it is believed that detailed investigations would reveal a definite relationship of this nature.

Although many decay fungi contributed to the deterioration of the looper-killed hemlock, only *Fomes pinicola* was found to be of major importance, both in number of infections and percentage of associated decay. This fungus attacked both sapwood and heartwood and was found to occur in all parts of the bole, although less extensively in the butt. The early infection and rapid spread of this fungus, as found by Foster and Hurn (1949), probably accounts for the relatively small number of infections and volume of decay associated with other fungi commonly attacking dead timber.

Although critical analyses of the principal associates of hemlock were not undertaken during the course of this study, a few Douglas-fir, Sitka spruce, and amabilis fir trees were examined to obtain a rough estimate of their rate of deterioration as compared with that of hemlock. It was evident from these examinations that amabilis fir was deteriorating equally as fast as hemlock, that Douglas-fir was considerably more durable, and that Sitka spruce was intermediary. These findings, although not conclusive, agree with those reported for the same species in other deterioration studies (Boyce, 1929; Buchanan and Englerth, 1940; Kimmey and Furniss, 1943).

The maximum length of time available for salvage of dead timber subsequent to a looper outbreak in stands of Vancouver Island hemlock will vary not only with rate of deterioration, but also with prevailing standards of utilization and with the value of the resource in relation to the product derived. Regardless of the end product, it is evident that salvage operations should commence immediately following verification that heavy mortality is to be anticipated. Otherwise, substantial reductions in recoverable volume can be expected to occur.

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A World Geography of Forest Resources

Edited for the American Geographical Society by Stephen Haden-Guest, John K. Wright, and Eileen M. Teclaff. 736 pages. The Ronald Press Company, New York. 1956. $12.50.

Review by G. Robinson Gregory
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Zon and Sparhawk's two-volume classic, *Forest Resources of the World*, has been out of print for a good many years. *A World Geography of Forest Resources* is the first real effort to fill the gap. While falling somewhat short of this mark, it succeeds in establishing several new ones of its own.

The book itself is a 31-article, 736-page symposium on world forest resources, each article having been prepared specifically for this publication. The 35 authors are, almost without exception, men who hold or have held positions of leadership in research, teaching, or administration in the countries about which they write. This gives to each chapter an authenticity and sense of intimate knowledge that more than compensates for the diversity of style that is inevitable in a compendium of this kind.

The five-chapter introductory section, sketching the role of forests and forestry in the world's economy, is followed by a region-by-region (and often nation-by-nation) description of the world's forests. The concluding chapter is devoted to an examination of future possibilities for forestry and for forest products. The many excellent charts and maps are newly-prepared for this volume, and the 108 photographs illustrating forest types are exceptionally well-chosen.

The professional forester will be disappointed at the shallow treatment accorded forestry principles and forest industries in the first section. Yet, if he reminds himself that the book was designed for lay readers, he will probably grant that the five introductory chapters cover the essential points in excellent fashion. And most foresters will find in Camp's chapter on "Forests of the Past and Present" information of a kind not usually presented in dendrological texts.

With respect to the main part of the book —that describing the world's forests—two observations may be offered:

(a) The coverage is decidedly uneven. For example, 36 pages are devoted to the Mediterranean region, while only 28 are given to the forests of the U.S.S.R. (where approximately one-quarter of the world's timber is located), and only 30 pages to all of South America. This inequality of treatment is unfortunate, yet probably reflects the current state of knowledge.

(b) For any area with which the reader happens to be really familiar, the coverage will probably appear quite superficial. Again, this seems eminently pardonable in a book attempting to give the significant aspects of the world's forests. The task of describing, for example, the forests and forest industries of the United States in 36 pages is no small one, and considered from this standpoint the reader may well be surprised at the detail and depth of some sections.

The final chapter by Erhard Rostlund is a well-written presentation of possible future product use, balanced against the current trends toward more intensive forest management.

In summary: here in one volume is a compilation of the major forest facts from nearly every country in the world. It represents a big job—one marred by unevenness of treatment—but still an extremely valuable and timely piece of work.

Some Distributions Encountered in Sampling Forest Stands

BY
J. H. G. SMITH
J. W. KER

WE WILL DESCRIBE some distributions that foresters encounter frequently when sampling forest stands, and will mention some of their problems and approaches. We hope that, through discussions such as these, statisticians will improve their understanding of the foresters' difficulties and will help them achieve more satisfactory solutions.

Given some knowledge of probabilities for single observations, we may draw important inferences about the best way of collecting and handling numerical data. Also, with a knowledge of the probability distributions that are most likely to be representative of our samples, we can relate our data to the work of mathematical statisticians. We can use their models, patterns of analysis, transformations, and can pay heed to their warnings concerning the proper use of these statistical aids, providing of course that we can understand the writings of the mathematical statistician.

If we do not find distributions and approaches to suit our data, we may derive some comfort from the statement that, for all but the most exceptional probability distributions, the mean of a given number (N) of values has a distribution that approaches the normal in form as N becomes large.

The nature of the distributions that we will encounter depends upon the variable under investigation and upon the size of the sampling unit. The two most commonly studied forest variables are *number of trees* and *volume per unit area*. Size of sample is governed by the number and size of the trees under study. Counts of reproduction are taken on plots only 0.001 or 0.004 acre in size. Volumes per acre are determined usually from plots 0.1 to 0.5 acre in size.

The usual approach in sampling of forset stands is to assess volume directly and carry a subsample for reproduction and other variables of interest. Most data are summarized by the means alone; a few standard deviations and coefficients of variation are calculated and all distributions are assumed to be normal, tending toward normal, or at least to have normally distributed means.

Reproduction Surveys

Many areas have been surveyed to assess the forest crop that is likely to follow after logging, burning, or both. Individual trees may be listed for each plot by species within classes of height or diameter. Alternatively, each plot or quadrat may be classified as *stocked* or *not stocked* depending upon the presence or absence of a tree of the desired size and species.

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Tallying by stocked quadrats often provides binomial distributions. If it is known that data can be described by the binomial theorem, complete description and interesting conversions are possible. For example, Grant (1951) has presented a mathematical method of converting the distribution from one quadrat size to that of another. Evans (1952) has shown how a frequency-density curve may be used to compare material obtained with quadrats of various sizes.

Numbers of seedlings per plot may be described by the Poisson distribution and thereby related to studies of that distribution in many fields of statistics. Ker (1954) has illustrated the application of the negative binomial distribution to *list-quadrat* reproduction surveys in the loblolly pine type.

Shanks (1953) has shown that conventional statistical treatment of small samples yielded biased estimates of vegetation in Appalachian stands. Logarithmic transformation was necessary to reduce or remove the bias.

Possible uses of the Bitterlich angle-count method in assessing stem distribution have been noted by Grosenbaugh (1952).

Spacing between individuals is an aspect of reproduction surveys that foresters seldom have considered; yet biologists and ecologists have attached great importance to this factor. Dice (1952) has suggested that spacing between individuals (distance to the nearest neighbour) could be used to describe the structure of populations and communities in quantitative terms. Clark and Evans (1955) have gone on to show how the nearest neighbour concept could be used to separate the consequences of social forces which cause clumping from other factors affecting the spatial patterns of distribution. There may be application of this approach in explaining the clumping of seedlings on favorable seedbeds.

The effect of kind of variable and size of sample upon the distribution of number of trees is illustrated in Table 1. The data represent the frequency distribution of alpine fir trees on 32 plots, each 0.016 acre in size, within a mixed forest of Engelmann spruce and alpine fir. The trees are segregated according to size into one class of advance reproduction, not over breast height (4.5 feet in height), and three classes of diameter at breast height (d.b.h.). In the advance reproduction class there are no zero counts, the plots containing from 4 to 31 trees. In the 0-5 in. d.b.h. class there are three zero counts and the number of trees ranges up to 9 per plot. The 6-11 in. d.b.h. class contains 11 zero counts and no plot has more than three trees of that size. Trees that are classed as 12 in. and larger in d.b.h. are sparsely distributed, do not occur on 19 plots, and no more than two trees of that size occur on any one plot. The pattern of occurrence of Engelmann spruce trees on the same plots differs considerably. Fewer spruce trees occur in the small size classes whereas considerably more merchantable trees over 12 in. in d.b.h. are present. The distributions of spruce and alpine fir trees differ among site classes and localities and depend greatly upon the age at which a stand is sampled. When the size of sampling unit is decreased, the number of zero counts in each size class increases greatly. Increasing the sample size to 0.2 acre, on the other hand, reduces the zero counts and increases the range in numbers within each diameter class. Further complexities are introduced into the frequency distributions when the trees are tallied in two- or one-inch classes of d.b.h.

The frequency distribution formed by the occurrence of plants on small plots or quadrats has frequently been compared with a Poisson series. Blackman (1935), using six- by six-inch quadrats, has found that the distribution of most species in certain grassland associations followed the Poisson series. However, the negative binomial provides a description of his data that is equally good and often superior to that of the Poisson.

TABLE 1. Frequency distribution of alpine fir trees on thirty-two 0.016-acre plots.

Tree size	Measure	Number of trees per plot															
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
		Number of plots															
3"-4.5'	Height	0	0	0	0	1	2	1	2	2	1	0	2	1	5	0	0
0"- 5"	D.b.h.	3	2	8	4	3	2	4	3	1	2						
6"- 11"	"	11	10	7	4												
12" +	"	19	11	2													

Tree size	Measure	Number of trees per plot (Cont'd)															
		16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
		Number of plots															
3"-4.5'	Height	0	1	1	1	1	1	1	2	2	1	1	0	0	1	1	1
0"- 5"	D.b.h.																
6"- 11"	"																
12" +	"																

Ker (1954) has shown that distribution series arising in quadrat sampling of loblolly pine reproduction in Arkansas are of negative binomial rather than Poisson form. He has also found that satisfactory agreement with the negative binomial is shown by coniferous seedlings that are restocking an extensive old burn on the Research Forest of the University of British Columbia at Haney. These analyses lead us to the conclusion that the negative binomial may prove to be far more useful than the Poisson distribution in the analysis of list quadrat studies.

The Poisson series arises with random sampling of a randomly distributed population when the probability of an event is exceedingly small and when a sufficiently large number of independent observations are taken to obtain a number of occurrences. Under such conditions the mean, m, may be assumed to be constant and equal to the variance, s^2. With the presence of clumpiness or heterogeneity, however, a contagious or negative binomial series arises.

The negative binomial has two parameters, the mean, m, and an exponent, k. Anscombe (1949) has given the formula for ϕ_0, the expected frequency of zeros in decimal form:

$$(1)\quad \phi_0 = N\left(1 + \frac{m}{k}\right)^{-k}$$

where N is the total number of observations, and the formula for ϕ_r, the expected frequency of any positive count, r, is:

$$(2)\quad \phi_r = \phi_0 \binom{k + r - 1}{r} \left(\frac{m}{m + k}\right)^r$$

The mean of the observed distribution y is used to estimate m, and k is estimated without error by the maximum likelihood solution of Fisher (1941) or by the simplified method described by Bliss and Fisher (1953). Ker (1954) has outlined and illustrated two approximate methods of estimating the parameter k, the efficiencies of which have been given graphically by Anscombe (1950).

Agreement of observed frequencies of number of seedlings on mil-acre quadrats with the negative binomial distribution is illustrated in Table 2. Despite the lack of efficiency of the approximate method

TABLE 2. Agreement of observed frequencies of number of seedlings on mil-acre quadrats with the negative binomial distribution.

Stocking percent	Basis, no. of quadrats	Computed statistics m	k	Efficiency of k-estimate, percent	Degrees of freedom n	Chi-squared	Probability, P
17.5	120	0.62	0.096	E>98	2	2.08	0.40
20.0	80	.35	.265	E>98	2	2.58	.30
50.0	120	1.96	.380	98>E>90	8	3.22	.90
85.0	200	6.76	.875	75>E>50	14	10.45	.70
92.5	40	16.88	.854	75>E>50	7	4.34	.75
97.5	40	8.15	2.60	E<50	10	16.69	.09
97.5	40	4.85	7.00	E<50	7	20.85	.005
	640				50	60.21	0.153

used to estimate the parameter k in the areas more than 50 percent stocked, the over-all chi-squared value at the bottom of the table shows no significant lack of agreement.

Of what practical use to the forester is such information? A relatively inexpensive stocked-quadrat survey of regenerating forest land, in which stocking is defined as the percentage of quadrats containing at least one established seedling, may be used to provide considerably more information concerning the forest reproduction. A knowledge of the relationship between the negative binomial parameters m, the mean number of seedlings per quadrat, the exponent k, and stocking percent, would permit us to predict the outcome of the more expensive list-quadrat survey. Perhaps only a person who is both a forester and a statistician can appreciate such a problem and make full use of statistical methods in this case.

When we have knowledge of the distribution we are sampling, we may take advantage of sampling plans such as those prepared by Oakland (1951). Oakland has drawn up sequential sampling schemes, sampling plans involving no fixed sample size, to provide effective sampling of distributions that are binomial, normal, Poisson, negative binomial, or negative hypergeometric in nature.

Sampling for Volume

Although volume per acre usually is the variable of prime interest, there are many approaches to its determination and many variables that may be studied with it. Volume per acre may be gross or net, may be for one or many species, may be for all or part of stands or individual trees, and may be estimated in units that range from board feet to cords per acre. Number of trees per acre, average diameter, basal area, stand age, site index and other variables may be of interest. Volume per acre may be uniform but most often is highly variable. Within any forest there is usually a gradient of volume resulting from systematic trends in quality of growth potential or site. Upon this trend will be imposed the end result of genetic factors and agents of mortality that may have operated more or less at random throughout the life of the stand.

Most studies of the sampling problems involved in assessing stand volumes have had as their objective the determination of the most efficient size and shape of plot. The best plot has been considered to be that which minimizes the coefficient of variation and the cost of establishment. Studies have been made by Hasel (1938), Johnson and Hixon (1952), Clark

(1953), and Savage (1956) for some typical western forest stands. Apparently, these investigators have not considered it worthwhile to study the actual distributions involved.

Johnson and Hixon (1952) presented data which may be used to show the influence of size of sampling unit upon frequency distribution of volumes. Their data for individual 0.025-acre plots are grouped in Table 3 by volume classes chosen to give at least 14 classes for each size of plot. The frequency distributions resulting from division of the plot data into equal volume classes are given also.

The nature of the frequency distribution ranges from nearly Poisson on 0.025-acre plots to approximately rectangular on 1.0-acre plots. The estimates of volume per acre on 0.025-acre plots range from 0 to 1.2 million board feet. When 1.0-acre plots are used, the volumes tallied per acre would range from 40 to 190 thousand board feet. We may wonder how adequately the coefficient of variation describes the relative variation of volumes per acre across such a tremendous range in frequency distributions.

The ease of use and apparent simplicity of the coefficient of variation may be misleading at times. In 640 acres of ponderosa pine forest the average coefficient of variation was only 35 percent for 64 one-acre plots. Yet coefficients of variation for 16 "forties" each containing 4 one-acre plots ranged from a low of 15 percent to a high of 120 percent.

Knowledge of distribution of volumes would be particularly important in determination of the optimum number of plots in a cluster comprising a day's work for one field crew. The components of variance should be known for the sources of variation "within" and "between" plot clusters. In this case we should not overlook the need for transformation of data prior to analysis.

Analysis of Variance

Many analyses have been made without any attempt to ensure that the data meet the basic assumptions of analysis of variance. Important results may be overlooked and false or misleading conclusions may be derived. Many foresters are suspicious of changes in data prior to analysis. Perhaps Quenouille's use of the word "scaling" is preferable to "transforming" of data prior to analysis (Quenouille, 1953). Suspicion and skepticism are understandable, in part, because the forester may experience difficulty in assessing the importance of differences in transformed data that have been shown to be statistically significant.

In certain cases there may be no scale that can handle the data adequately. What can one do with 39 zeros and 24 one-hundred-percents in observations of percentage survival on 240 seed spots?

When it is possible to work with known distributions, the problems of transformation and analysis are simplified. We need the help of statisticians to provide further classification and evaluation of many distributions of stand variables which are of interest to foresters.

Harmonization of Distributions

Studies of volume, growth, and yield often require harmonization of distributions that are exceedingly complex. The problem is relatively simple when distributions are normal and may be harmonized mathematically or graphically on arithmetic probability paper. Skewed distributions are more common and much more difficult to deal with, but skewed distributions have been harmonized graphically on arithmetic probability paper or by development of alignment charts with one curved axis.

Meyer (1930) considered these graphical methods and found that they fail to represent the true conditions because they force a set of curves of varying form into a set having but a single form. He found that the graphical methods gave good re-

TABLE 3. Size of sampling unit and its relation to the distribution pattern of old-growth Douglas-fir volumes.

Volume Class, Scribner Dec. C (10's of bd ft)	Plot size, acres					
	0.025	0.10	0.20	0.225	0.30	1.00
	Number of plots					
0	425	3				
1-25	255	6				
26-50	137	7		1		
51-100	93	12	1			
101-200	94	21	3	2		
201-300	104	22	4	4		
301-400	86	18	3		1	
401-500	105	29	4	7	1	
501-600	87	36	6	5	1	
601-700	70	24	4	4	3	
701-850	65	38	11	4	3	
851-1000	36	36	9	9	2	
1-1000	1,132	249	45	36	11	
1001-1250	21	46	18	12	5	
1251-1500	13	31	24	15	7	
1501-1750	4	17	25	7	9	
1751-2000	3	17	17	19	12	
1001-2000	41	111	84	53	33	
2001-2500	1	27	22	25	26	
2501-3000	1	10	16	22	15	
2001-3000	2	37	38	47	41	
3001-4000			28	21	22	
4001-5000			5	10	13	5
5001-6000				2	12	5
6001-7000						3
7001-8000						8
8001-9000						3
9001-10,000						3
10,001-11,000						2
11,001-12,000						1
12,001-13,000						3
13,001-14,000						2
14,001-15,000						1
15,001-16,000						1
16,001-17,000						
17,001-18,000						2
18,001-19,000						1
Totals	1600	400	200	169	132	40

sults for standard deviation and coefficients of variation but that the trend which characterizes the coefficient of asymmetry and excess was replaced by a constant. This fault would be especially serious in the small diameter classes because of their usually large negative asymmetry of distribution. Meyer went on to demonstrate the application of Charlier's curves of types A and B to a number of diameter distribution series in eight different species.

No doubt statistical research will reveal other ways in which a knowledge of distributions will prove useful to foresters.

Concluding Discussion

In most forestry problems it is difficult to assign definite single-factor objectives. The forester usually tries to find out a little about a number of aspects of the forest he must manage.

We would like to know more about distributions that we may encounter commonly. We believe that it would be much easier for foresters to use these if they were completely investigated and described by statisticians. On the other hand statisticians have not outlined clearly the means by which knowledge of our forest distributions may be used in designing effective plans of sampling. Should minimizing coefficients of variation and the elements of time and cost continue to be our main objectives?

We would like to know also a great deal more about the character of the exceptional probability distribution in which sample means may not be normally distributed. We would like to know the influence of sample size on this important question and we need guidance in learning how to recognize where special care in sampling is necessary. The possible limitations of the use of the coefficient of variation to summarize spread or scatter should be determined.

Transformation should be made more useful to the forester and more understandable to the layman.

There is a great need for close contact between foresters and statisticians in order that statistical methods may be used more effectively in forestry. One of the largest handicaps in this regard is difficulty in the translation of mathematical approaches into solutions for our problems. We need forester-statisticians rather than foresters with a smattering of statistics and statisticians with no appreciation of the problems of the forester.

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Soil Fertility and Fertilizers

By S. L. Tisdale and W. L. Nelson. The Macmillan Co., N.Y. 430 pp. 1956. $7.75.

Review by Robert E. Dils
University of Michigan, Ann Arbor.

In *Soil Fertility and Fertilizers*, an excellent text is provided for a beginning course, treating nearly all phases of the subject. The text is designed for students of agriculture. Its 19 chapters and 430 pages are conveniently arranged into six major topics.

Following a brief historical introduction, two chapters deal with plant growth and nutrition. Four chapters are devoted to a discussion of the forms and behavior of specific elements nitrogen, phosphorus, potassium, calcium, magnesium and sodium as well as secondary and trace elements. The manufacture and properties of various specific and mixed fertilizers are covered in five chapters after which farm manure and liming are treated. The final five chapters deal with soil fertility evaluations and the use of fertilizers in management programs.

Technical subject matter is discussed in a clear, concise manner and the text is well supplied with illustrative charts, graphs and tables. At the end of most chapters there is a list of questions designed to focus attention on the important points covered in the text.

Since the text was written for the agricultural student, the forester will not find a treatment on the fertilizing effects of forest litter and humus or macro- and micro-organisms. Similarly, discussions of soil fertility and the application of fertilizers to forest soils are not covered.

However, the text provides a very useful tool for the forest nurseryman or the forest researcher delving into the field of forest soil fertilization.

Initiation and Development of Flower Primordia in Slash Pine

BY
FRANÇOIS MERGEN
LOLA E. KOERTING

SLASH PINE (*Pinus elliottii* Engelm.) is one of the most important forest tree species of the Southeastern part of the United States. As a result of its importance, several public, private, and educational organizations in this country and abroad are working with slash pine as the major species in their fores tree improvement programs. It is imperative that the flowering and fruiting cycle of this species be known so that cultural methods can be developed to produce flowers in a more regular pattern on selected trees, and on trees growing in seed orchards. The pollination and fertilization patterns have been fully described for several species of the genus *Pinus*, but a systematic study of the time of flower primordia initiation, and a detailed morphological description of the rudimentary male and female flowers has not been made for pines. There have been a number of experiments which attempted to manipulate the flowering mechanism in pines by nutritional and other means. The timing of these treatments could only be guessed at for little precise information was available on the initiation of flower primodia.

The present paper presents the results of a study which was made to determine the time of initiation of male and female flower primordia and the subsequent floral development of these structures on slash pine trees growing in the Lake City, Florida area. For the microsporangiate strobili, the steps leading to the formation of microspore mother-cells are described, and the description of the megasporangiate strobili includes the various phases from flower primordia initiation to the first indication of an ovular swelling on the ovuliferous scale. The descriptions were discontinued at these stages because an excellent study of their further development was described by Miss Ferguson in 1904. The dates given in the present paper are for collections made in the Lake City, Florida area.

Literature Review

In his detailed treatise "Die Coniferen und die Gnetaceen," published in 1872, Strasburger reported that the primordia of the male strobili of *Pinus Pumilio* (*P. mugo* Turra var. *Pumilio* Zenari) are laid down during the early part of August of the

The authors are located at the Yale University Forestry Research Center, John A. Hartford Foundation Program in Forest Biology, Valhalla, N. Y. Mergen is Asst. Prof. of Forest Genetics; Koerting is Research Associate. The collection of the buds was started while the senior author was stationed at the Lake City (Fla.) Research Center of the Southeastern Forest Experiment Station, U. S. Forest Service. The authors thank P. E. Hoekstra and E. E. Miles for carrying out some of the field collections.

year preceding pollen shedding, and that the primordia of the female strobili are initiated in late August or early September. He stated that the rudimentary megasporangiate flowers over-winter with only the bracts developed and that during April of the next year the initials of the ovuliferous scales become evident. In 1904 Ferguson reported that "with the exception of *Pinus Strobus*, the staminate cones, in the pines which I have studied, make their appearance in October or November." With reference to the pistillate strobili of the hard pines which were included in her study she observed that "it is possible that in these species they were organized in the autumn, but I have not been able to find any evidence that such is the case. I have recently, November 25, 1902, attempted to discover the young cones of *Pinus rigida* and *P. austriaca*, but, as formerly, the search was futile." Coulter and Chamberlain (1910) reported that in *Pinus Laricio* (*P. nigra* Arnold) growing in the Chicago area, the ovulate strobilus begins to develop in late fall and winter. Chamberlain (1935) did not give any dates for the various developmental stages in conifers but he mentioned that they will vary from species to species and even within a species depending on regional climates. He presented a schematic drawing of a longitudinal section through a young staminate cone of *Pinus banksiana* which was collected on September 10. The sporangia in the bottom section were in the early sporogenous stages, and the archesporial cells had not been differentiated in the apical part of the cone. Doak (1935) presented an average annual curve for the deposit of units on the long axis for *Pinus*. He placed the deposition of the staminate cone series near the end of July, and that of the ovulate cones during the middle of August. In his paper, "The earliest stages of pinon cones," Little (1938) reported that he found the first evidence of primordia of the cones in dormant buds which he had collected during November.

Since Strasburger published his results (Strasburger, 1872 and 1879) no further detailed studies of the first stages of the developing microsporangiate or megasporangiate strobili in *Pinus* have been made, although there are several reports for other members of the *Coniferales*. Dupler (1919 and 1920) described in detail the staminate and ovuliferous structures of *Taxus canadensis* with respect to their development and vascular anatomy. Allen (1941) reported that for Douglas fir, western hemlock, and grand fir differentiation of reproductive organs takes place during the time when vegetative growth has ceased, and that reproductive buds can be clearly distinguished from vegetative buds towards the end of August. The ontogeny of the microsporophyll in Douglas fir was described in a later paper by Allen (1946) but he did not give the dates which corresponded with the various developmental stages. However, in a drawing made from a microsporangiate strobilus collected on August 12, he illustrated the arrangement of the sporophyll primordia. In an earlier paper (Allen, 1943) he had indicated that for Douglas fir growing near Victoria, British Columbia, the male and female strobili are differentiated during the month of August.

Ferguson (1904) described in detail the sporogenesis of several species of pines. She reported that, with the exception of *Pinus strobus*, the primitive archesporium was clearly differentiated in the autumn but that the microspore mother-cells did not arise until the latter part of April. However, Coulter and Chamberlain (1910) reported that in *Pinus laricio* the mother-cell stage usually is reached in October with the exception of early winters when the staminate strobili may pass through the winter in the late stage of the sporogenous tissue. *Pinus sylvestris* also passes the winter approximately in the mother-cell stage (Haydon, 1907).

The ontogeny of the sporangia has been the topic of discussion since 1880, when Goebel referred to the parent cells of the sporogenous tissue as the archesporium. Allen (1946) critically reviewed the perti-

nent literature and attempted to trace the differentiation of the microsporangium proper in *Pseudotsuga*. He was unable to detect a hypodermal archesporium in Douglas fir microsporophylls as had been described by Chamberlain (1935) for some of the conifers. By the time he was able to recognize the sporogenous tissue, it was four to six cells in from the hypodermal layer.

The early investigators who studied and described the growth and anatomy of strobili of pines during the 19th century were mainly concerned with the evolution and morphology of these structures. They attempted to interpret them in the light of the angiosperm flowers and the spore-bearing structures of the ferns rather than to describe their detailed development. The literature on the interpretation of the microsporophylls and cone scales is very extensive and has been reviewed on numerour occasions (Coulter and Chamberlain, 1910; Doak, 1935; Thompson, 1940; and Florin, 1954). In studying bisporangiate cones, several of the early investigators attempted to identify the steps which lead to the evolutionary sequence of the reproductive structures in conifers. Doak (1935) made a comprehensive review of the literature on this subject, and on the basis of a study of some thirty-five species of pines, he reinterpreted the evidence already available and added significantly to the knowledge of the evolution and ontogeny of the axial and foliar systems in *Pinus*. He concluded that "the staminate cone axis is considered homologous to the dwarf shoot, and the ovulate cone axis homologous to the long shoots," and that "the ovulate cone is considered a compound strobilus and the cone scale a simple strobilus." The reader is referred to this monograph for an extensive treatise on the subject.

Characteristics of Reproductive Structures in Slash Pine

Slash pine is a monoecious species and the sporophylls are borne in separate strobili or cones: the megasporangiate (♀) and microsporangiate (♂) strobili. Both the male and female strobili are borne over the entire crown area, but the female flowers occur most abundantly in the upper part of the crowns. Often the male aments are missing from the uppermost branches in the crowns. The male and female flowers are subterminal in nature, the male flowers occurring at the basal portion and the female flowers occurring on the apical portion of the current year's growth. At the time of pollination the male aments are sometimes separated from the female strobili by as much as five inches of sterile branch growth. The male flowers become visible to the naked eye around the middle or latter part of October and the female flowers can be recognized during December. The male flowers occur in clusters of up to eight aments and are arranged spirally around the axis of the branch. When ready to shed their pollen during the latter part of January and during February, they are up to 5 cm. long and have a diameter of ¾ to 1 cm. Soon after dehiscence is completed, the aments wither and fall from the tree. The female flowers develop in a ring close to the terminal bud and occur in groups of 1 to 6. However, up to 14 cones in one ring have been observed. Occasionally two rings of cones, separated by up to 2 cm. of sterile branch growth, are found in slash pine. This is the result of two distinct periods of female strobili initiation. The ovulate cones are receptive to pollination during the latter part of January and during February. The period of receptivity of an individual flower varies from several hours to up to a week, depending on weather conditions. At the time of pollination they have a flesh color and are about 2.5 cm. in length. Seed ripens during the fall in the year following pollination.

Bisporangiate strobili have been observed on several slash pine trees in the Lake City, Florida area. In every instance, the basal part of the hermaphroditic structures bore microsporophylls, and the apical part bore ovuliferous scales with apparently normal ovules. An instance of particularly high

frequency of bisporangiate strobili was noticed in a 20-year-old slash pine plantation in which increased flowering had been brought about by a heavy application of commercial fertilizer. Bisporangiate strobili in pines have been adequately described in the literature and will not be discussed in this paper (Goebel 1880, Strasburger, 1872; Doak, 1935; and Zobel and Goddard, 1954).

Materials and Methods

The buds for this study were collected at weekly intervals during the period from May 1954 to January 1955, from slash pine trees growing in an open old-field stand in the Olustee Experimental Forest in Baker County, Florida. The trees which were used had well-developed crowns and the collections were made from the distal branches in the upper part of the crown. Collections were restricted to trees which were flowering actively during the preceding years, and buds were collected only from branches which bore both male and female flowers in the previous two years. A weekly collection consisted of five buds each from five trees. The trees were climbed with the aid of a Swedish ladder and the buds were placed directly in the fixing agent. Formalin-acetic acid-ethyl alcohol (FAA) was used as a killing and fixing agent. The buds were dehydrated in an alcohol-chloroform series and embedded in Tissuemat (56°C). Some of the longer bud scales were clipped off just before embedding to facilitate the sectioning. The slash pine scales exhibit extensive fraying with interlocked marginal fringes which make it difficult to obtain perfect serial sections. The scales cling together very tenaciously and these can be unwound in ribbon-like fashion. Serial sections were cut on a rotary microtome at thicknesses ranging from 10 to 15 μ. Four types of staining techniques were used: haematoxylin and safranin; safranin and fast green; tannic acid, iron chloride, safranin, fast green; and haematoxylin and aniline blue. Smears of the latter developmental stages were stained with acetocarmine. The sections were mounted in Permount for future reference.

Results

A. *Formation of staminate cone.* In the buds collected during May and early June no evidence of primordia of staminate strobili was noticed and the apical point of the bud was somewhat rounded (Fig. 1A). In some of the collections the apical point had elongated considerably and by June 11 had assumed a more pointed shape. Cell division was very rapid at this stage as evidenced by the number of mitotic figures in the apical area. In one of the buds collected on June 25, a distinct swelling could be observed in a axil of a partially formed cataphyll before the cataphyll had reached its full size. The tissue in these mounds of cells was undifferentiated during the early stages, but by July 12 a row of vascular tissue was evident in the lower vegetative areas of the primordia (Fig. 1B). By July 19 differentiation of vascular tissue had progressed toward the apical portion of the rudimentary ament as can be seen in the lower primordia in Figure 1C. During the latter part of July the lower meristematic area started to differentiate hood scales which began to envelop the rudimentary strobilus and by September 13, up to eight layers of scales had formed (Fig. 1E and F). The innermost layer pushed between the primordia and the previously formed scales, curving inward near the apex, and formed a protective arch. These scales have a thick epidermis, especially in the outer surface, which becomes suberized early during development. Several of the scales which formed last, the involucral scales, elongated only slightly. At this stage the strobili primordia had not formed a protective cuticle and this hood should prevent excessive evaporation from the succulent structure. During this period of growth, the only change recognizable within the primordia proper was a broadening, and a lengthening of the axis of the rudimentary ament. Additional meriste-

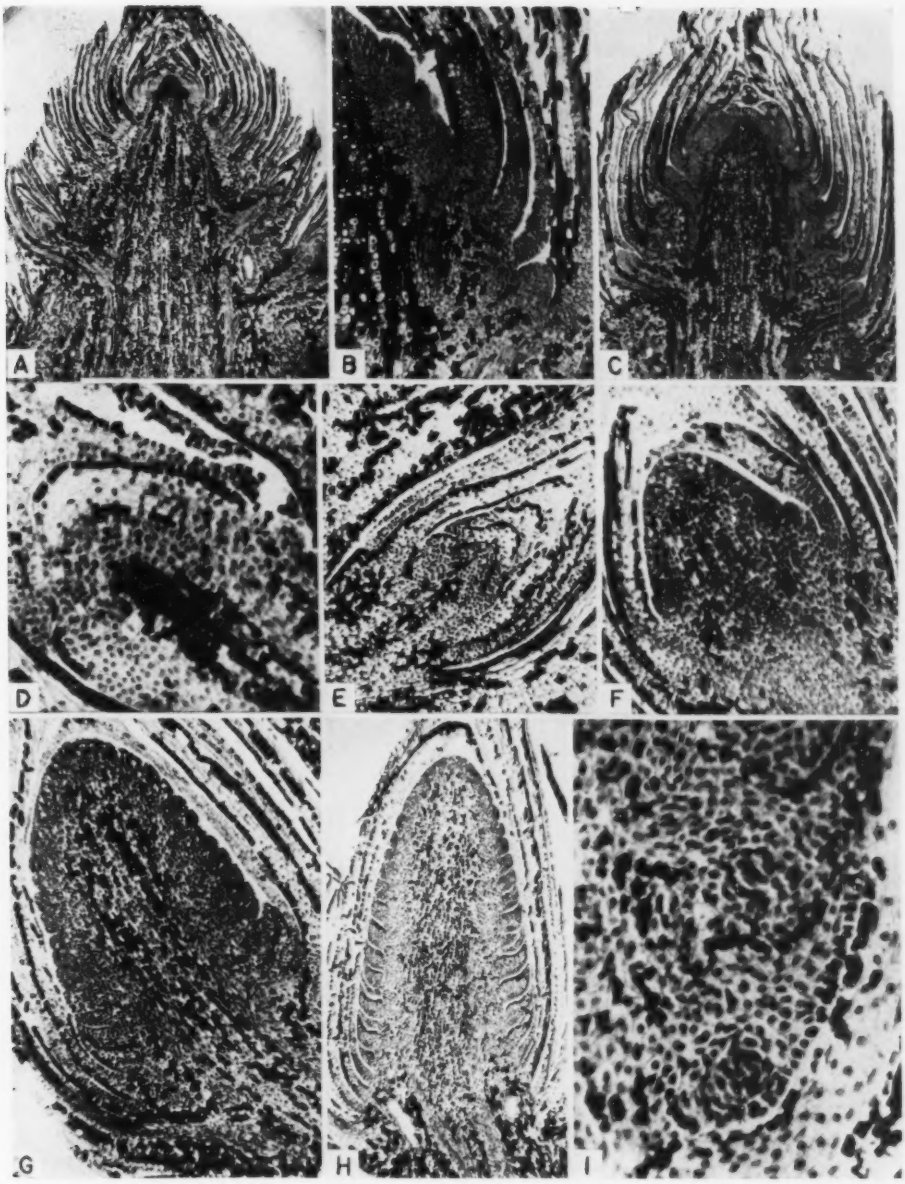

FIGURE 1. Development of the staminate cone. A. *Section through bud collected May 25 showing sterile series (×7).* B. *Primordia (♂) in the axil of a cataphyll; July 12 (×18).* C. *Section through bud collected July 19. Four ♂ flower primordia in various stages of development are visible (×30).* D. *Vascular differentiation in ♂ primordia; August 9 (×84).* E. *Protective hood formed by the scales over the developing ♂ primordia; September 13 (×38).* *Hood scale primordia forming at base of developing ♂ ament; September 13 (×53).* G. *Initiation of rudimentary microsporophylls on ♂ ament; October 11 (×31).* H. *Differentiation of microsporophylls; October 25 (×24).* I. *Sporogenous tissue in basal part of microsporophyll; November 1 (×120).*

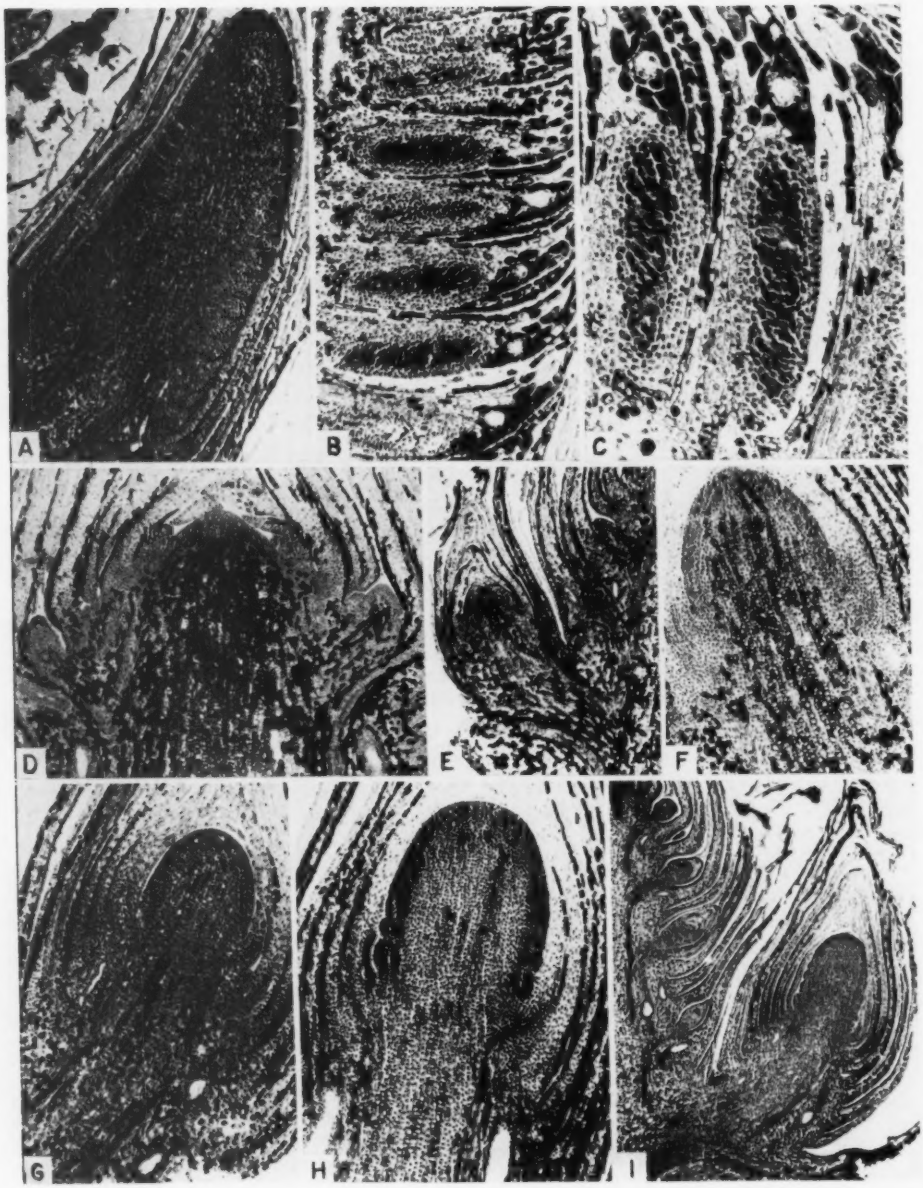

FIGURE 2. Development of staminate and pistillate cone. A. *Male ament collected November 1 (×24).* B. *Microsporophylls in ament collected December 14 (×41).* C. *Microsporophylls containing microspore mother-cells; December 14 (×75).* D. *Primordia of ♀ flower on bud collected September 17 (×26).* E. *Pistillate strobilus enveloped with hood scales; October 4 (×15).* F. *Differentiation of vascular tissue in midrib area of ♀ strobilus; October 18 (×32).* G. *Vegetative stalk on ♀ flower; November 1 (×32).* H. *Initiation of bract scale primordia; November 15 (×35).* I. *Condition of female flower collected November 22. Details of vegetative bud are plainly visible (×10).*

matic activity became pronounced during the latter part of September. It resulted in a lengthening of the axis of the strobilus and the rudimentary microsporophylls started to differentiate at the base. During the early stages they are similar in appearance to the primordia of the hood scales and their axis it at a right angle to the main axis of the strobilus (Fig. 1G).

During the remainder of the month of October differentiation of microsporophylls progressed towards the apex and the first formed microsporophylls started to turn upward (Fig. 1H). This was the result of asymmetrical growth: cell division, both periclinal and anticlinal, was more rapid in the abaxial area than in adaxial surface. In several of the buds collected on October 4, sporogenous initials had been laid down in the abaxial part of some of the early microsporophylls. In several of the sections, the sporogenous initials had already given rise to sporogenous tissue. These cells were larger in diameter, had a denser cytoplasm and accepted more stain than the surrounding cells (Fig. 1I and 2A). The midrib or main axis was well marked by vascular bundles which connected the upper part of the rudimentary microsporophylls with the vascular system of the developing branch. Further, the outer layer of cells surrounding the microsporophylls, with the exception of those cells in the area of the sporogenous cell activity, had become suberized and accepted the safranin stain. This monocellular layer eventually forms the "epidermis" which surrounds the microsporophylls.

The sporogenous tissue enlarged considerably during the month of November. In some of the microsporophylls which had formed first, the microsporangia appeared to be fully developed in early December. By December 14, the pollen sacs were filled with well-defined microspore mother-cells which originated from the sporogenous tissue. They were surrounded by a tapetal layer consisting of three or four layers of cells (Fig. 2B and C). At this stage a resin canal, complete with epithelial and sheath cells, had formed at right angles to the stalk close to the scale-like terminal appendage of the microsporophylls.

In the Lake City, Florida area the male strobili passed the winter in the microspore mother-cell stage and the reduction division occurred during the middle of January. At that time, the aments were about 1.5 cm. in length. Subsequent development from this stage on is very rapid, if weather conditions are favorable. Aments collected over a three-day period from the same tree during the latter part of January, showed all stages from the microspore mother-cell stage, through the tetrad stage, to the second vegetative division of the microspore.

B. *Formation of the pistillate strobilus.* The primordia for the female strobili are not laid down as early as those of the male catkins. The first evidence of pistillate flower primordia was observed during the latter part of August. They first became noticeable as slight protuberances in the axis of a developing cataphyll (Fig. 2D). This mass of cells was pointed, and vascular tissue in the central axis started to differentiate without any delay. The protecting bud scales started to develop in a manner similar to that described for the male flowers. They continued to envelop the protuberance in a spiral manner until a tight hood had formed (Fig. 2E). By October 18, a hood of up to 12 layers of scales was observed around some of the primordia. During this period of growth, there was pronounced differentiation into vascular tissue in the midrib area, and the apical part of the primordia assumed a more flattened appearance. The vegetative stalk also elongated considerably and formed xylem and phloem elements, and both longitudinal and horizontal resin canals appeared (Fig. 2F and G).

The primordia of the bracts started to form during the latter part of October and were accompanied by active meristematic activity in the basal part of the rudimentary pistillate strobilus (Fig. 2H). They appeared as lateral outgrowths or papillae and

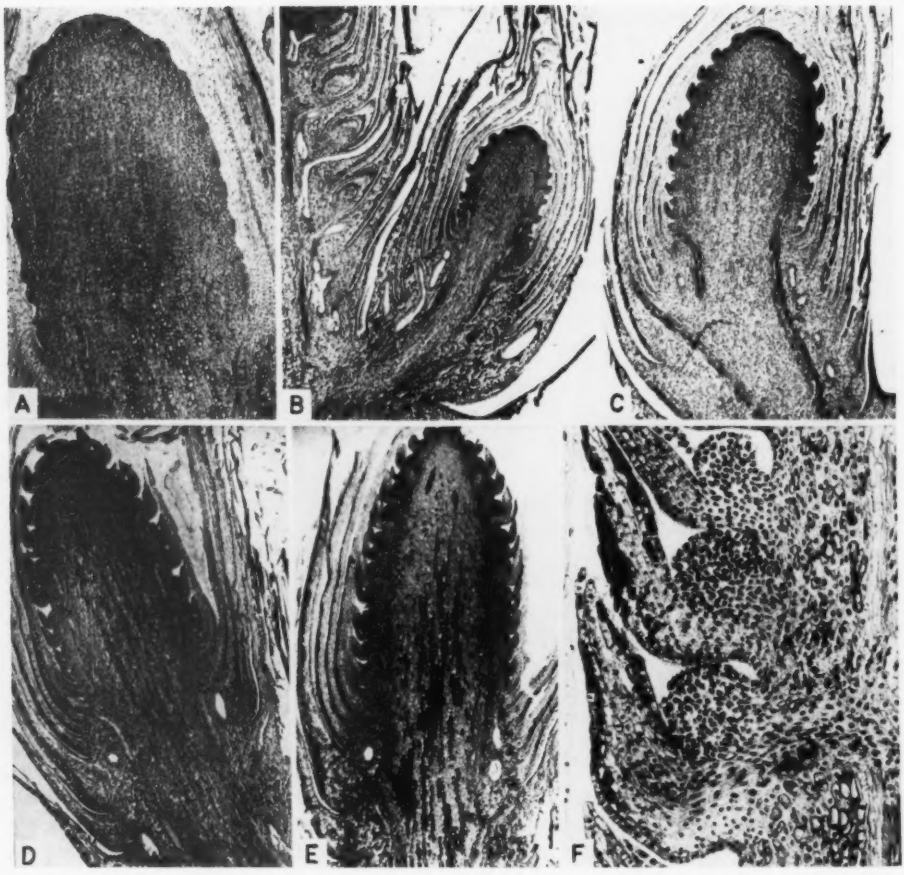

FIGURE 3. Initiation and development of ovuliferous scale. A. *Rudimentary female strobilus covered with bract scale primordia; November 29 (×25).* B. *Development of the bract scales; December 22 (×9).* C. *Initiation of ovuliferous scale in axil of bracts; December 30 (×11).* D. + E. *Further differentiation and growth of ♀ strobili; December 30 (×11).* F. *Well formed bract scales subtending the developing ovuliferous scales which contain the ovular initials; January 6 (×72).*

progressed in an acropetal direction. They were formed by both periclinal and anticlinal cell divisions (Fig. 2I). This developmental period continued for a period of about three weeks. After this time the developing strobili were covered with slight protuberances which were arranged in a spiral manner (Fig. 3A). Vascular tissue had formed in the rudimentary bracts of the lower region; this tissue was connected to the vascular elements of the midrib area. During the later stages of growth, cell elongation and cell division was more rapid in the lower region, causing these bracts to curve slightly upwards towards the apex of the strobilus (Fig. 3B). The ovuliferous scale arose in the axial of a bract and first appeared as a conical mass of cells during

the latter part of December (Fig. 3C, D, and E). Initiation of these primordia also progressed in an acropetal direction. Buds collected on January 6 showed well-defined mounds of cells which were subtended by the bracts. Vascularization in the midrib, as well as in the bracts, had progressed rapidly and the epidermal cells of the bract had begun to cutinize (Fig. 3F). There was distinct cell organization in the upper and inward part of the ovuliferous scale. Rapid cell division, as evidenced by a large number of mitotic divisions resulted in the formation of a protuberance. This was the first indication of the organization of an ovule. In this ovular swelling were contained the sporogenous initials which will give rise to the sporogenous tissue. At this stage, which was about three weeks before pollination, the partially developed strobilus proper was 4- 4.5 mm. in length, and the total length of the structure including the stalk and the hood was 12 mm. The strobilus was still completely enclosed by the interlocked hood scales and was whitish in color.

Discussion

The time of primordia initiation of slash pine strobili in the Lake City, Florida area was in close agreement with that given by Doak (1935) for the pines he had studied. The microsporangiate strobili, however, made their appearance one month earlier than was indicated by Doak. There are several reasons for this. Doak was not mainly interested in the precise period of initiation, the curve he represented was an average for several species of pines, and unless studied closely the primordia of the male strobili are hard to distinguish during the very early stages. During their first period after initiation they undergo little outward change which is distinguishable under the microscope when conventional staining techniques are used. Until a diagnostic staining method is developed it will be necessary to work in reverse and start with a male catkin which can be clearly recognized and view the sections in backward order until the first signs of primordia are found. The megasporangiate strobili, on the other hand, can be recognized much easier by their broad axis and by their subsequent rapid development. Another factor which makes it difficult to detect the initiation proper relates to sectioning of the buds. During the early stages there are no outward signs and, therefore, the buds have to be sectioned blindly. Unless the primordia are located on the periphery of a longitudinal section and have their axis in the same plane as that of the section they cannot be recognized with certainty. This probably accounted partly for the failure by Ferguson (1904) to find any evidence of the strobili in hard pines during the fall preceding their emergence.

The microsporangiate strobili were initiated during a period of about six weeks, while that of the female strobili was limited to about two weeks. In the samples studied there was only one distinct row of female strobili.

The period of initiation and development as given is applicable only for slash pine trees in the Lake City, Florida area for the specified year. The climatic and site conditions within the natural range of slash pine are varied and therefore affect their growth. As a result the period of initiation will fluctuate not only from year to year but will also vary over the range of the species. Therefore, the results of this study can be applied in another area only with modification. For this reason the reproductive characteristics of slash pine, with particular reference to the Lake City area, were given so that comparison with other regions or even with other species can be made.

During the course of this study no evidence of a hypodermal origin of the sporogenous initials as described by Ferguson (1904) and Chamberlain (1935) was observed. At the time these cells could be distinguished with certainty there were several layers of cells inward from the hypoderm. The ontogeny of the sporangia in

Pinus needs further study as has been suggested by Allen (1946).

There was a definite resting period for the microsporangiate strobili and they passed this period in the microspore mother-cell stage. This was of interest because some of the pines from the northern latitudes reach the same developmental stage before winter dormancy sets in. The female strobili, on the other hand, did not rest during the winter but continued their growth. Those species of pines which grow in more southern latitudes, *e.g.* in Mexico, and shed their pollen during the fall probably have a continuous developmental period for both their male and female strobili.

The information obtained will be valuable not only in research work with this species but also should be helpful to the forest manager. The research forester can use these results to time the start of flower induction trials, to time the pruning of experimental trees in seed orchards so that he will have a large number of potential flower-bearing branches, and to relate environmental and biotic conditions to the production of flowers. To the forest manager, on the other hand, these results will be of help during the timing of his cuts to convert a stand into a seed production area, or during intermediate fellings which are aimed at bringing about an increased seed crop.

Summary

The initiation and development of microsporangiate and megasporangiate strobili in slash pine were investigated.

For slash pine trees growing in Baker County, Florida, the male strobili started to form near the end of June and kept on forming for a six-week period. Their differentiation and growth until the stage when the microspore mother-cells are formed are described and illustrated.

Female strobili were initiated during the latter part of August and their growth is described up to the stage when the ovules are formed. The various stages of development are illustrated.

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Contribution Toward a Study of Douglas Fir Beetle Development

BY
J. P. VITÉ
J. A. RUDINSKY

THE TIME REQUIRED for development of the immature stadia of a destructive insect must be known in order to understand its population dynamics and its relationship to parasites and predators, as well as to provide the basis for prognosis or control. Effective control measures against bark beetles in particular depend to a great degree upon the proper timing of their application.

Field observations of the length of development of the Douglas fir beetle, *Dendroctonus pseudotsugae* Hopk., have been made by several authors in the past, as will be noted later. Concerning these observations, naturally, one must draw conclusions upon the course of local climate from the situation and year of observation and make only rough estimates of the temperature conditions prevailing during the observations. It seemed appropriate therefore to perform experiments, apart from field observations, in order to establish the duration of particular immature stadia in the Douglas fir beetle development. The experiments were limited by the means and time at our disposal to development under various constant temperatures. Many interesting questions had to be left open, such as the effect of variable temperatures upon the rate of development of the immature stadia, the effect of high and low temperatures upon the maturation of the gonads and the reproductive potential, and the effect of various relative humidities upon the whole development.

Material, Rearing, and Methods

The present study was made from November, 1955, to September, 1956. The beetles used came from Douglas firs that were cut in the early spring of 1955 in the Oregon State College McDonald Forest (elevation 800 feet) and infested in late May. Young adults were present by the middle of August. Portions of infested logs (3 feet long and 10 to 11 inches in diameter with ½-inch thick bark) were sealed at the ends by wax and kept in the insectary until used in the laboratory.

The adults emerged from the bark after the infested logs had been exposed to 22° C. in a greenhouse for various periods of time. Emergence from logs brought into the greenhouse in November began after two weeks' exposure and continued over

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four weeks, with peak emergence at the end of the second week. The time of exposure necessary for emergence of the beetles at 22° C. decreased in reverse ratio to the length of the insects' hibernation. Thus, five months later, for instance, on the second of April, the peak of emergence occurred six hours after the logs were brought into the greenhouse, and all emergence was finished in one day. Each log portion yielded around 350 beetles and about 45 parasitic wasps, *Coeloides brunneri* Vier. The emerged beetles were collected daily in plastic-screened cages, and only beetles that had emerged in the last 24 hours were used for new infestation in the experiments.

Portions of fresh Douglas fir logs (3 feet long, 10 inches in diameter), sealed by wax, were placed in plastic-screened cages (39 in. × 37 in. × 26 in.) in a greenhouse, and the beetles were introduced for attack. (Because of good light conditions in the greenhouse, uniform distribution of attacks was assured, in contrast to the uneven distribution of attack in the laboratory.) After preliminary experiments it was decided to use only 80 beetles for each log portion; a greater number of beetles, particularly over 150, resulted in considerable mortality of brood because of overcrowding. The beetles, introduced into cages with fresh log portions, were kept in a greenhouse at 22° C. for 24 hours, during which time, except for a few individuals, they bored in. The beetles found outside the log at the end of 24 hours were removed; thus all attacks were made on the same day. The freshly attacked logs were kept in the greenhouse an additional 12 hours, in which time copulation usually took place and the first eggs were laid. Precautions were also taken that no parasitic or predatory insects were introduced. The newly infested log portions were then placed at various constant temperatures for developmental studies. The relative humidity ranged between 50 and 60 degrees. Experiments were repeated at least twice except for the experiment at 11° C. (Fig. 3). About 1600 adults were used and some 8900 larvae and pupae examined.

To establish the developmental duration of particular stadia at different constant temperatures, the duration of each stadium at 21.5° C. ± 1° C. was first found. Several egg galleries were opened periodically (daily at high temperature) at the point of attack, and only the most advanced stadium or instar, originating from the first four eggs, was considered for the developmental time; in the case of instars, newly molted larvae alone, with totally white head capsules, were used to fix a time limit for terminating the previous instar and beginning the following one. At 29° to 30° C. the galleries were examined at half-day intervals during the first two instars, where the developmental time is comparatively short. In addition to these periodical examinations of immature stages under the bark, eggs, larvae, and pupae were reared under various constant temperatures in vials filled with moist, ground inner bark, for comparison with the development under the bark.

The head-capsule widths of instars were measured with a calibrated micrometer at a magnification of 90× to the nearest 0.0085 mm., and in order to avoid possible distortion of newly molted instars, only measurements of the larvae with well chitinized head capsules were used for graphical presentation.

Development of the Immature Stadia

A necessary condition for intensive study of the rate of development is precise knowledge of the particular stadia, their number, and their morphological characteristics. Moreover, it is important to the experimental technique to differentiate between developmental phases within particular stadia if possible, and to establish their duration. By controlled experiments, it is possible to establish precisely the age of a developing individual and to predict exactly the time necessary to complete its development. Also, comparative experiments under different temperatures are more effective, quicker, and often more exact, particularly with sensitive experimental animals, than experiments under field conditions.

Also, it is often easier to find the duration of particular phases by short experi-

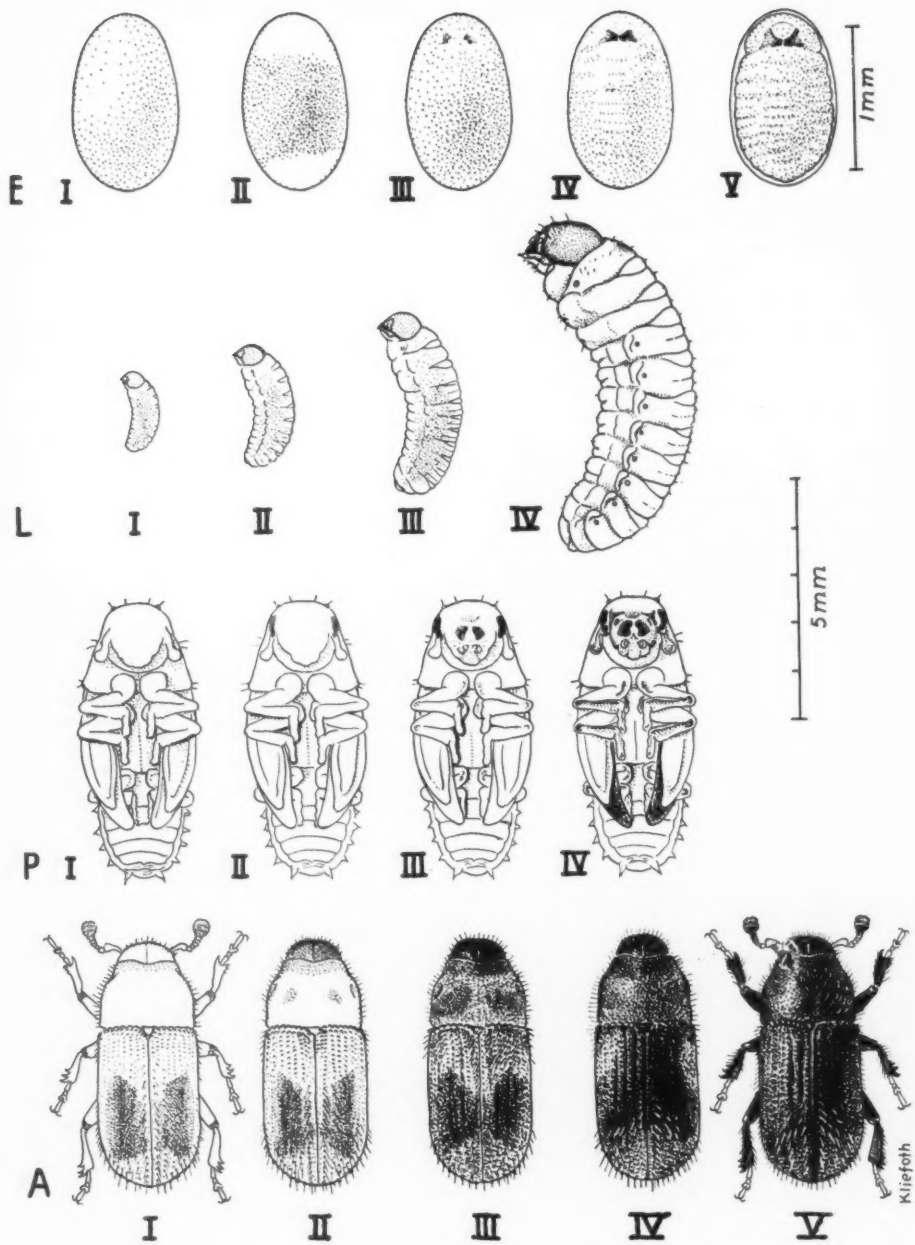

FIGURE 1. *Development of the Douglas fir beetle: characteristics of the immature stadia and the young adults. Explanation in text.*

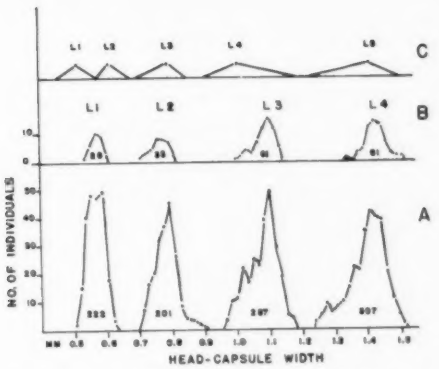

FIGURE 2. *Widths of head capsules in the instars of the Douglas fir beetle. A shows the total head-capsule measurements; B the measurements of larvae from one gallery only; and C the results given by Bedard (1933).*

ments than by controlled rearing of the whole stadium. This is particularly true for the low temperatures with long developmental periods. In this way, moreover, one can gain detailed information to supplement the main experiments, in which the durations of particular stadia are established by rearing all the stadia consecutively.

To insure conditions as close to natural as possible, rearing methods were used as described above. As a check, bark was removed over galleries of exactly dated attack at periods established experimentally. Part of the stadia or phases thus found were used for measurement, and part were reared in vials with small inner bark pieces, and also as recommended by McMullen,[1] as control for the next stadia. Rearing by another method, in which inner bark was pressed between glass or cellophane plates, brought no usable results. The rates of development of all stadia and phases were observed at 29° and 21.5° C.; the following description of the immature stadia and phases refers to development at 21.5° C. ± 1° C.

[1]L. H. McMullen, presented at the Seventh Annual Western Forest Insect Work Conference, Dec. 1955, Spokane, Washington.

Egg stadium. The first externally recognizable indication of embryonic development occurs after 15 hours at 21-22° C. Then the egg is no longer evenly milk white, but instead against the light it shows a slight solidification in the center with a large transparent space in the cephalic end and a similar but smaller space in the caudal end of the egg (Fig. 1, E I and II). This phase lasts about four and a half days. Next, the widely opened and weakly chitinized mandibles are visible through the chorion, and after six hours they close together and darken (Fig. 1, E III and IV). Within ten more hours, the egg passes over gradually into the last phase, in which the other head appendages can be recognized as well (Fig. 1, E V). Within 6 hours usually the larva hatches, as the dried chorion breaks where cut by the mandibles.

Larval stadium. The freshly emerged larva is recognizable by its white head capsule and its pointed abdomen. With the first intake of food, the alimentary canal begins to take on the red color of the consumed inner bark, as is apparent through the transparent larval cuticula. At the same time, the abdomen shows the typical rounded form of the bark beetle larvae. There are four instars, and the larvae of all are similar in form and color until the full-grown larva in the fourth instar empties its digestive tract and reaches the non-feeding, prepupal stadium (Fig. 1, L I, II, III, and IV). The body of the larva in this quiescent stage becomes again uniformly white, and the abdomen is contracted to a compact, cylindrical form.

The particular instar reached by a larva can be determined in two ways: by measuring the head capsule or by examining the larval galleries for the remnants of head capsules left from previous molts. Within the same population, at least, the instars can easily be determined by the size of the head capsule. The data from 987 single head-capsule measurements are given in Fig. 2.

The instars of some of the measured individuals were first assessed by observation. In the "white stages", the newly hatched larvae and the prepupal larvae are recognizable without difficulty; the "reddish stages" are also easily recognizable by the number of head capsules found in the individual larval galleries. The necessary condition for this latter method, of course, is that the attack on the stem is normal and does not result in overcrowding, and further that the bark is taken off cautiously so that all of the larval galleries of the same groove can be examined and compared. Locating the head capsules is made easy by the fact that they usually lie in characteristic places. One finds them among the frass and chewing material in the larval galleries at relatively constant distances from the egg niches.

At 21.5° C. the head-capsule remnants of the first instar lay an average 9 mm. from the niche; the head-capsule remnants of the second instar lay 17 mm. farther away; and those of the third instar lay another 24 mm. away. The head-capsule remnants of the fourth instar naturally lay in the pupation chambers, which were constructed no farther than 35-40 mm. from the third molting place. When there was sufficient free space, the average length of a larval gallery was 85 mm.; yet its length seems to depend on the temperature under which the development took place.

The total larval development, from eclosion to pupation, was accomplished in about 30 days, from which the first instar (L 1) took 3 to 4 days, the second (L 2) 5 days, the third (L 3) 6 days, and the fourth (L 4) 15 days, with about 7 days spent in the reddish, feeding phase and 8 days in the quiescent, prepupal phase.

The five instars reported by Bedard in 1933 and 1950 seem less attributable to regional differences in the biology of the Douglas fir beetle than to an erroneous assumption. It should not be necessary to say that the value of Bedard's basic work scarcely suffers thereby. The mistake involved here can be explained by Bedard's method of calculating the width of head capsules (1933) and his assumption that the intervals between the extremes of the head capsules increase from the first to the last instar instead of decreasing (Fig. 2). The number of instars presented here agrees with that recently reported.[2]

Pupal stadium. The pupal stage lasts from 9 to 10 days at 21.5° C. The second half of the development can easily be followed externally. On the snow-white pupa, the compound eyes become slightly visible after 4 or 5 days (Fig. 1, P I and II), and after another 2 or 3 days, the eye cornea can be seen clearly. Simultaneously, the mandibles begin to darken slightly and after a day become quite distinct (Fig. 1, P III), while the body gradually assumes a yellowish color and the elytra acquire a more or less distinct dark marking (Fig. 1, P IV). The pupa remains in this stage for 2 days, after which the skin on the head and thorax is ruptured, and the callow adult emerges.

The immature stadia, their phases, characteristics, and developmental times are summarized in Table 1.

The various immature stadia differ considerably in the actual time required for their development. As can be seen in Table 1 and Fig. 3, the fourth instar requires the longest time for its completion. This can easily be understood, since the fourth instar is actually a double stadium (feeding and prepupal phases) where the greatest growth and also basic tissue transformation take place.

Development under various constant temperatures. The Douglas fir beetle was reared under 7 constant temperatures. The times required for egg, larval, and pupal development at those temperatures are given in Fig. 3.

Temperatures above 32-34° C. after considerable exposure are lethal to eggs and first-instar larvae, thus exceeding the upper developmental limit, and temperatures below 8° C. prevent observable embryonic development. The fastest complete development from the egg to the emer-

[2]K. H. Wright and L. H. McMullen, presented at the Seventh Annual Forest Insect Work Conference, Dec. 1955, Spokane, Washington.

TABLE 1. Immature stadia and phases of the Douglas fir beetle, their characteristics, and duration at 21.5 ± 1° C. (extremes in brackets).

Stadium	Phase	Characteristic	Duration	
			Days	Hours
Egg	I	Uniformly milk white		15 (12-18)
	II	Central solidification	4-5	
	III	Mandibles open and indistinct		6
	IV	Mandibles closed, distinct		10
	V	Head capsule distinct		6
1st instar	white reddish	Head-capsule width: 0.573 mm. (0.508-0.622)	3-4	
2nd instar	reddish	Head-capsule width: 0.790 mm. (0.710-0.880)	5	
3rd instar	reddish	Head-capsule width: 1.10 mm. (0.962-1.160)	6	
4th instar	reddish	Head-capsule width: 1.44 mm.	7	
	white-prep.	(1.23-1.50)	8	
Pupa	I	Snow white	4-5	
	II	Eyes barely visible to distinct	2-3	
	III	Eyes and mandibles distinct	1	
	IV	Elytra dark	2	

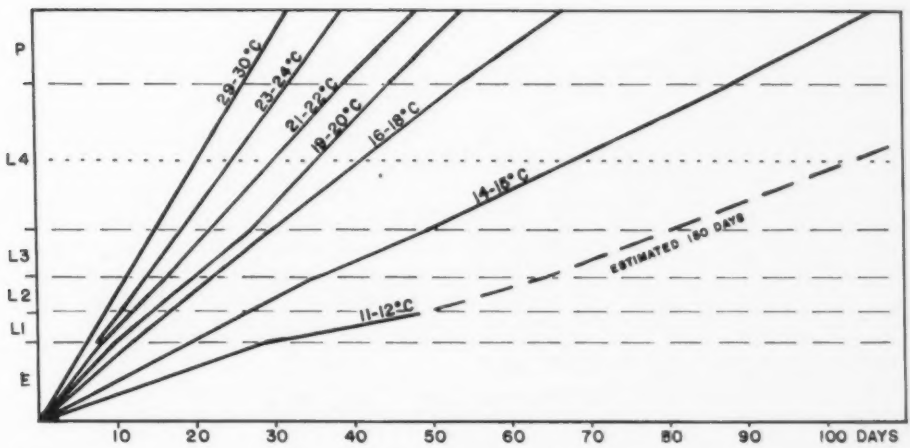

FIGURE 3. *Developmental duration of the immature stadia under several constant temperatures. The dotted line divides the fourth larval stage into its two phases: the reddish, feeding phase and the non-feeding, prepupal phases.*

gence of callow adults occurred in 33 days and took place at 29-30° C. The egg stage lasted 6 days; the first instar, 2.2 days; the second instar, 2.8 days; the third instar, 3.5 days; and the fourth instar, 13 days (of which 6 days were spent in the feeding phase and 7 days in the quiescent, prepupal phase). The pupal stadium itself lasted 5.5 days.

At low temperatures the duration of the total development increased progressively, and particularly below the temperature of 17° C. it shows a distinct increase.

Field Observations

The development of immature stadia of the Douglas fir beetle in the forest takes place under fluctuating or variable temperatures. The great diversity of temperature conditions resulting from regional differences, seasonal climatic conditions, altitude, exposure, stand composition, forest canopy, and the condition of the host tree, gives the beetle an unlimited variety of developmental conditions.

In the past, several authors have made field observations on the duration of development of the Douglas fir beetle; in most cases, however, they were not correlated with existing temperature conditions. Nevertheless, they convey an idea of the length of development under a variety of field conditions.

Chamberlin (1918) reports the incubation of eggs lasting from 15 to 21 days, with 16 days for the majority. The larval stage required 9 to 14 weeks in the same locality. Chamberlin states that he "has been unable to account for the great variation in the length of the larval stage except that it may be due to the condition of the host tree. Altitude and latitude cannot be held responsible, since the extremes have been noted the same year, in the same locality, and on the same site but never in the same log" (p. 18). Although all logs used for the observation had been attacked at the same time, the logs where larval development took 14 weeks were older than those with 9 weeks' larval development.[3] It appears, therefore, that the retardation in development was caused by the dried-out condition of the older logs as compared to the fresh ones; a food scarcity probably resulted from the greater cambium deterioration, and also the humidity might have been lower than in fresh logs.

Bedard,[4] studying the seasonal history of the beetle in northern Idaho and northeastern Washington, states that 91 days were required to complete all immature stadia. The durations of the stadia were: eggs 8 days; first, second, third, fourth, and fifth instars 6, 13, 16, 16, and 17 days respectively; and the pupal stadium 8 days.

Of particular interest are observations made by K. H. Wright[5] in 1953 in three areas in Washington and Oregon. The three study areas and the developmental duration from egg laying to tender adult stage were as follows:

1. Packwood Lake Trail (near the town of Packwood, Washington): elevation 1800 feet; northwest aspect, moderate to heavy shade. The developmental duration was 120 days, from which about 40 days were spent in the egg stage.
2. Johnson Creek (about 5 miles south of the Packwood Lake Trail): elevation 1800 feet; steep southern aspect, light to moderate shade. The length of development was 95 days.
3. Upper Siuslaw River (10 miles southwest of Elmira, Oregon): elevation 700 feet; level, moderate shade. The developmental time was 80 days.

It is important to realize that 1953 was a very cool season, especially in the spring and early summer, a fact which prolonged the developmental time, particularly that of the egg stadium.

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[3]Personal communication.

[4]W. D. Bedard. The Dougals-fir beetle—its seasonal history, biology, habits, and control. U.S.D.A., Forest Insect Field Station, Coeur D'Alene, Idaho. Unpub. rep. 1933.

[5]Personal communication.

TABLE 2. Developmental temperatures and duration of immature stadia of the Douglas fir beetle under field conditions (compare Fig. 4).

Stadium	Duration in days	Ave. day temp. in ° C.	Ave. night temp. in ° C.	Mean temp. in ° C. (day and night)
Egg	24	14.0	10.4	12.2
L1	6	17.5	13.5	15.5
L2	8	16.5	12.5	14.5
L3	8	19.6	14.2	16.9
L4	19	21.0	16.4	18.7
Pupa	11	18.6	15.0	16.8
Total development	76	17.5	13.5	15.5

In 1954 Wright made comparative observations in the Cascade Mountains and the Oregon Coast Range and found the time of development to be 90 and 70 days respectively. He observed the first attacks in the Coast Range on April 15, whereas in the Cascades the first attacks were made one month later.

McCowan and Rudinsky[6] reported three weeks' retardation in the development of immature stadia in shaded logs as compared with exposed logs under otherwise equal conditions. Also, the development on a south slope was accomplished two weeks earlier than that on a north slope, in both instances with logs under a closed canopy.

In 1956 two experiments (A and B) were set up in McDonald Forest, near Corvallis, elevation 1000 feet, no exposure. In experiment A the canopy was about 50 percent open because of windfalls during the previous winter. The fallen trees were attacked on May 14 when, for the first time in the spring, the temperature reached 20-22° C. and remained there for 6 hours (see Rudinsky and Vité, 1956). The development in these logs took 64 days. For comparison, trees were cut on May 17 in an adjacent stand, and development in logs under a completely closed canopy was observed (Experiment B). The daily tem-

[6]V. F. McCowan and J. A. Rudinsky, Biological studies on the Douglas fir bark beetle, Millicoma Forest, Coos Bay, Oregon. Progress report. Weyerhaeuser Timber Company, Tacoma, Washington. Forestry Research Notes. 1954.

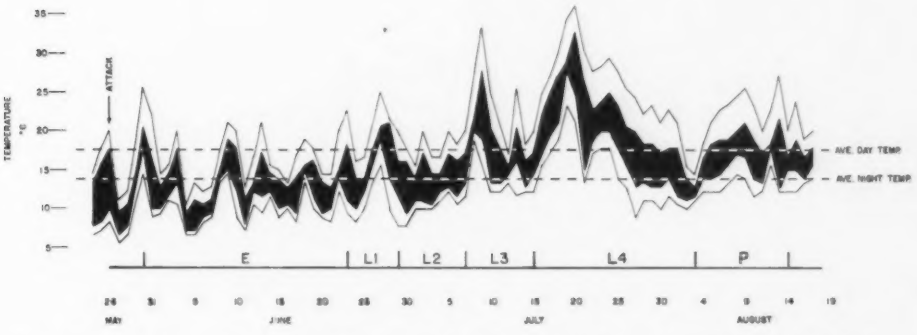

FIGURE 4. *Development of the immature stadia of the Douglas fir beetle as related to the temperature in the field. Explanation in text.*

peratures on this plot were 4 to 5° C. lower than those on plot A, and the development took 76 days. The developmental duration of each stadium as related to the recorded air temperature in experiment B is given in Fig. 4 and Table 2.

The upper line in the graph (Fig. 4) represents the daytime maximum and the lower line the night minimum temperatures in °C.; the upper limit of the dark field represents the average daily temperatures (from 8 AM to 6 PM), and the lower limit the average night temperatures (from 8 PM to 6 AM).

Maturation

From the abundance of open questions concerning the sexual maturation of the adult and the reproductive period of the Douglas fir beetle, only three points were taken: (1) the external course of the maturation of young adults, (2) the development of the ovaries, and (3) the sex ratio and its effect on the reproductive potential.

The external course of maturation. The freshly emerged callow adult does not possess mature sexual organs, nor has it yet a hardened skeleton. It gains both during a maturation period in which it feeds extensively on the inner bark around its pupation chamber. The maturation is evident externally by the change in the color of the skeleton. At 21-22° C. the yellowish-white callow adult, whose eyes, mandibles, and bases of the antennae are alone distinct, turns gradually yellow during the 5 or 6 days following its emergence. During this time, the head and the pronotum turn light brown (Fig. 1, A I and II). After another 4 or 5 days this light yellowish-brown tone has extended over the entire body and appendages, during which time the head and pronotum have again become browner (A III). The light color darkens during the following 4 or 5 days, particularly on the elytra, which definitely turn dark brown and completely hide the flying wings (A IV). The young beetle in this stage can be recognized by the opaline yellowish-brown color on the thorax and sterna. Complete coloration of the body is achieved after two weeks (A V), but even before then the young beetle may become sexually mature and also capable of flying.

One can roughly place maturing young beetles in either the light, sexually immature phase (time of development 2 weeks at 22° C.), or the dark, mature phase. A characteristic useful in identifying the light phase is that the flying wings are still visible through the elytra.

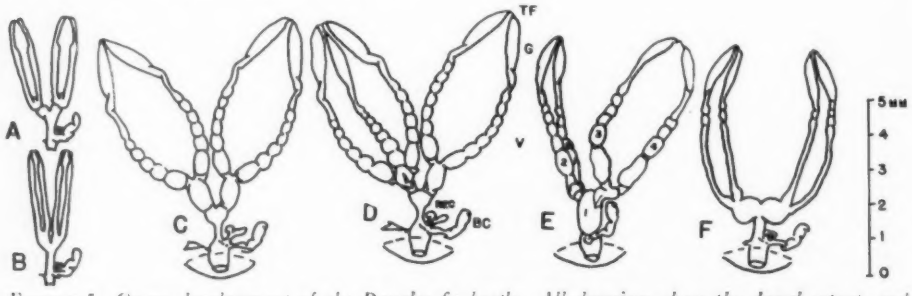

FIGURE 5. *Ovary development of the Douglas fir beetle. All drawings show the dorsal aspect, and the times indicated refer to 21.5° C. A shows the ovaries in the advanced pupal stadium, and B in a 2-day-old adult. C shows the normal ovaries, and D an anomaly of three ovarioles, each in an adult newly emerged from the bark. E shows the ovaries of a young female near the end of the first egg-laying period (3 weeks after emerging from the bark), and F the ovaries of a regenerating female after finishing the first egg-laying period (6 weeks after emerging from the bark). BC is the bursa copulatrix, REC the receptaculum seminis, V the vitellarium, G the germarium, and TF the terminal filament.*

The development of the ovaries. The gonads, which develop progressively during the larval stage, are already easily recognized during the first pupal phase. The ovarioles become short slender tubes, a process which begins in the pupal stage and continues into the first phase of the adult stadium (Fig. 5, A and B). Thereafter follow the differentiation of germarium around the vitellarium and the production of eggs. About three weeks after pupation (at 21-22° C.), the ovarioles are filled with ripening eggs (C). In addition to the usual symmetrical structure of the ovaries, often an anomaly appeared in the beetles examined by us, in that one ovary consisted as usual of one pair of ovarioles, but the other consisted of three ovarioles (D). It was found that the females with this anomaly had a higher daily egg production than those with normal ovaries.

The rate of egg production, like the maturation of the egg, depends upon the temperature. At 21.5° C., in the beginning of the reproductive period the females lay on the average 4 to 7 eggs daily, although individual variations are fairly great. With the progress of the egg-laying period, the daily number of eggs decreases considerably, so that near the end of the period (after 2 to 3 weeks) a single egg was laid. The total number of eggs per gallery was usually between 30 and 60, although occasionally almost 300 were found. The control of the number of eggs produced daily is comparatively simple. If an egg gallery is opened cautiously along its side (so that none of the eggs are damaged) and kept at the same temperature, the number of eggs laid daily can be concluded from the number of eggs hatched daily. That a correspondingly high air humidity must be kept is obvious.

After all the eggs have been laid, both oviducts are usually enlarged, and by this fact the old regenerating female can easily be distinguished from the young female (Fig. 5, F).

The sex ratio. Although Bedard[4] clarified the sex ratio of the Douglas fir beetle in 1933, later confusing reports were made on the numerical relationship of males and females. Indeed, the sex ratio is 1:1, as is easily proved by examining the young adults before they emerge from the bark. In freshly attacked trees, on the other hand, the males are outnumbered by females in the ratio of 2:3, as found by Bedard, or 1:1.33, as expressed by DeLeon.[7]

To explain this fact, Bedard proved that old females making a second attack do not require a second fertilization, and therefore when they mix with young females in the new attack they are usually not followed by males. Also, another cause for the decrease in ratio is the longer exposure of the males to predacious insects and their greater mortality, by which the ratio might be reduced to 1:2 as occurred in Bedard's experiment. We believe that a similar cause lies behind the smaller number of young males also: their greater activity leads not only later to higher mortality, but already during the first flight some males are lost in their wide spreading. In other words, during the flight the females must find only favorable breeding materials, whereas the males must find not only the trees attacked by females but also their entrance. In addition, the merely temporary stay of the male in one gallery (for several days, seldom for longer than 2 weeks), together with its search for another female, increases its exposure to predators.

An important question, therefore, is how far the reproductive potential can be affected by the smaller number of males. Two of Bedard's statements are important in this connection: in their second attack, old females "are capable of laying fertile eggs without another fertilization" (p. 7),

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[7] D. DeLeon. Notes on the biology of the Douglas fir beetle in the Central Rocky Mountain Region. U. S. Dept. Agric., Forest Insect Laboratory, Fort Collins, Colorado. Unpub. rep. 1940.

TABLE 3. Effect of the sex ratio upon the reproduction.

Experiment	Number of beetles introduced ♀♀	Number of beetles introduced ♂♂	Number of beetles recovered ♀♀	Number of beetles recovered ♂♂	Number of parent galleries A total	B with fert. eggs	C unfert. eggs	D no eggs
A	12	2	10[3x]	1	9	1	6	2
B	12	3	11[3x]	2	14	3	5	6
C	12	4	11[3x]	5[1x]	11	6	2	3
D	12	6	11	6[1x]	11	8	3	----
E	12	8	10	4[1x]	11	10	----	1
F	6	5	6	5	7	6	----	1
Total	66	28	59	23	63	34	16	13
			—9	—3				
			50	20				

[x]Found outside the bark, most of them dead.

and more important "one male sometimes fertilizes more than one female" (p. 8). There is then the probability that the lack of males is made up by the bigamy or even polygamy of at least some of them. To study this question, young beetles were introduced into fresh Douglas fir logs at 22°C. in six different sex ratios (ABC DEF). The beetles were distinguished in sex according to the greater roughness of the females' elytral declivity, a method that allowed merely slight error only because a sufficient number of beetles with pronounced characteristics were used (see Chapman, 1955, p. 2). After 2 weeks the logs were examined; the results are given in Table 3. The sex of all beetles found (not all of the introduced beetles could be recovered) was ascertained by section. The logs contained three types of galleries: galleries with fertilized eggs, mostly with developing larvae (B), galleries with unfertilized eggs (C), and galleries with no eggs at all (D). These latter were mostly short, curved galleries.

The results of the experiment are somewhat obscured by the fact that some of the beetles did not bore in and died outside the bark, and some were lost. Nevertheless, when one considers the data concerning the recovered beetles and their sex, it follows that of 50 females 34 were fertilized and 16 not (= 50 galleries with eggs = sum of B and C). The fertilization was performed by at least 20 males, at most by 29, and probably by 25 males. In other words, a sex ratio of 4:5 would have secured complete fertilization. This represents the minimal quota, because in the last two experiments (E and F) the females were not at all abundant enough to prove the capacity of the males. In experiment D, 6 males were able to fertilize 8 females; thus a ratio of 3:4 insured the fertilization.

Females that were not followed by males frequently abandoned the already finished gallery, bored in again at another place, and finally laid unfertilized eggs. Such eggs can be easily recognized by their failure to develop: they gradually dry out and later show black spots.

Even though this experiment can be only orientative, it shows, nevertheless, that the lack of males (which, according to field observations, is not less than the ratio of 2:3) is equalized for the most part by the bigamy or polygamy of individual males, and therefore does not necessarily influence the reproductive potential.

Summary

The Douglas fir beetle was found to go through four instars. The developmental

duration of the immature stadia, their phases, and characteristics were studied in the laboratory at 21.5°C., and the duration was also established at various constant temperatures. A brief comparison was made with the development under field conditions. The ovaries were found to mature during the pupal and tender adult stadia, and females were discovered with anomalous numbers of ovarioles, which increase their egg production. The uneven sex ratio in attacked trees does not seem to influence the reproductive potential of the Douglas fir beetle.

Acknowledgment

Acknowledgment is due to Mr. Richard Kliefoth, Hann. Münden, Germany, for drawings in Figure 1; to Mr. J. R. Pierce, graduate assistant in forest entomology, Oregon State College, for his help on the field phase of this investigation; and to Mr. K. H. Wright, Pacific Northwest Forest and Range Experiment Station, for permission to use his unpublished data on Douglas fir beetle development under field conditions.

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Errata

In Studies of attack of Ambrosia beetles in softwood logs on Vancouver Island, British Columbia by M. L. Prebble and K. Graham (FOREST SCIENCE 3: 90-112), the following errors occurred: on page 102, table 6, the caption should read "holes" and not "lots" and "galley" should be "gallery"; on page 104, col. 1, line 22 should read "in no instance"; on page 104; col. 1, line 24, "Table 5" should be "Table 6"; on page 105, col. 1, line 6, the words "In explanation of these" were omitted.

Seasonal Height Growth of Deciduous Trees

BY
THEODORE T. KOZLOWSKI
RICHARD C. WARD

FOREST TREES have been shown to have seasonal height growth patterns which vary markedly with different species. Species differences occur not only in total amounts of growth but also in the lengths of growing seasons. Kienholz (1941), for instance, divided deciduous species of Connecticut into two distinct groups on the basis of their height growth characteristics. In the first group he found that height growth accelerated rapidly to a late May climax and fell off to zero by late June. The whole growth period lasted only about 60 days. About 90 percent of the year's growth occurred in a four-week period which began one or two weeks after growth started. In this group Kienholz included maples, red oak, white ash, and beech. In the second group, growth began at about the same time but did not accelerate as fast. The climax for this group occurred in Connecticut in mid-June and fell off to zero by the middle of August. Kienholz's data showed that 90 percent of this group's growth took place in a sixty-day period beginning three to four weeks after growth started. Characteristic species of the group included grey and white birch, yellow poplar, and the aspens. Generally similar species variations and seasonal growth patterns were found in New York state by Cook (1941).

Although height growth of trees is determined by interactions of hereditary potentialities and a complex of environmental factors to which trees are exposed, the length of the growing season and the shape of the growth curve of a species are apparently controlled most by hereditary factors and appear to be relatively independent of normal fluctuations in environmental factors. Severe droughts and excessively low temperatures may check growth but usual moisture and temperature variations can actually have little effect on the seasonal pattern (Kramer, 1943).

Pronounced differences in seasonal growth curves of deciduous forest tree species have been shown to occur widely (Illick's (1919) data for Mont Alto, Penn-Johnston, 1941; Kienholz, 1941; Kramer, 1943; Reimer, 1949; Kozlowski, 1955).

Another salient feature of tree growth is the relatively small fraction of the frost-free season that is devoted to height growth. Illick's (1919) data for Mont Alto, Pennsylvania showed that about 90 percent of all shoot growth took place in the first quarter of the frost-free season. Both Kramer (1943) and Kienholz (1941) em-

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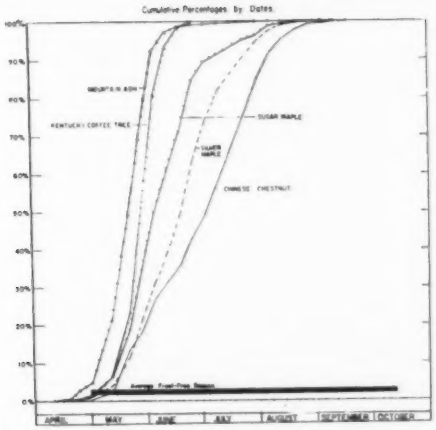

FIGURE 1. *Course of seasonal growth of 5 deciduous species during 1954 at Westfield, Mass. Growth plotted as per cent of season's total completed at various dates.*

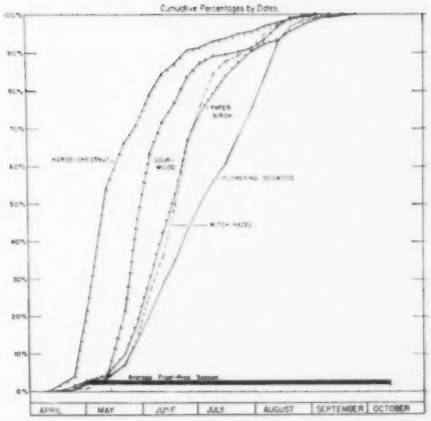

FIGURE 2. *Course of seasonal growth of 5 deciduous species during 1954 at Westfield, Mass. Growth plotted as percent of season's total completed at various dates.*

phasized that height growth occurs in only a small part of the frost-free season. A few species, however, utilize most of the frost-free season for height growth.

The present work was initiated to see whether the marked seasonal variations in height growth patterns of different species in plantations and in the forest would manifest themselves under nursery conditions in soil of high fertility and known physical characteristics. Another objective of the present work was to see whether young trees in soil of high fertility under normal nursery management would utilize much more of the growing season than they normally do in competition in the forest. It was also desirable to obtain additional height growth data for deciduous trees in central Massachusetts for comparison with data from other regions.

Methods

Ten species of deciduous trees varying in age from 2 to 10 years were used. The trees were widely spaced for maximum development and were growing in a soil of high fertility under regular nursery management at the Adams Nursery, Westfield, Massachusetts. The soil was Chicopee fine sandy loam with a moisture equivalent of 6.83 percent and a permanent wilting percentage of 2.45 percent. The selection of species was based on availability and it was not possible to obtain different species of the same age. However all individuals of the same species were of the same age. The species used were: sugar maple (*Acer saccharum* Marsh), silver maple (*Acer saccharinum* L.), Chinese chestnut (*Castanea mollissima* Blume), Kentucky coffee-tree (*Gymnocladus dioicus* (L.) K. Koch), mountain–ash (*Pyrus americana* (Marsh.) D C.), paper birch (*Betula papyrifera* Marsh.), witch–hazel (*Hamamelis virginiana* L.), flowering dogwood (*Cornus florida* L.), sourwood (*Oxydendrum arboreum* L.) D C.), and horse-chestnut (*Aesculus hoppocastaneum* L.). Twleve trees of each species were chosen and there was some mortality as well as loss due to removal. Late in March each tree was marked with paint ten centimeters from the tip of its terminal bud and tagged with a number. Measurements of height increase were made at approximately weekly intervals until October 2nd when all growth had ceased.

TABLE 1. Height growth data for 10 deciduous species during 1954 at Westfield, Mass.

Species	Av. orig. height	Av. increment	Percent increase	Growth started	Growth stopped	Duration of growth	When 5% completed	When 95% completed	Middle 90%
	cm.	*mm.*				*weeks*			*days*
Sugar maple	60	1,040	173	May 1	Aug. 28	17	May 9	July 23	75
Silver maple	133	1,038	78	Apr. 24	Sept. 11	20	May 13	Aug. 1	80
Chinese chestnut	77	903	117	Apr. 24	Aug. 28	18	May 14	Aug. 13	91
Ky. coffee–tree	95	510	54	Apr. 19	June 26	10	May 9	June 14	36
Mountain–ash	69	502	73	Apr. 19	Aug. 7	16	May 1	June 9	39
Paper birch	141	374	27	Apr. 19	Sept. 11	21	May 13	Aug. 19	98
Witch–hazel	87	313	36	Apr. 24	Aug. 28	18	May 15	Aug. 7	84
Flowering dogwood	118	197	17	Apr. 24	Sept. 4	19	May 15	Aug. 18	95
Sour-wood	75	143	19	Apr. 24	July 31	14	May 13	Aug. 10	89
Horse-chestnut	23	81	35	Apr. 19	Aug. 28	19	Apr. 24	July 24	91

Results

There was much difference in the amounts of total growth between species, but since the trees varied in age and size some of the differences are obviously attributable to age alone. Therefore in this work emphasis is placed on seasonal growth patterns only, and all data are given in terms of percentages of the total seasonal growth for purposes of species comparisons.

Cumulative growth during the growing season. Figures 1 and 2 show what percentages of total seasonal growth had been completed by each date during the growing season. Additional pertinent growth data are given in Table 1. The species in Figure 1 were grouped together since they made the greatest amounts of absolute growth. Those in Figure 2 made much less total growth.

Mountain–ash showed a very early start and a long protracted finish due to bud elongation. Ninety percent of its growth occurred during 39 days from May 1st to June 9th.

Kentucky coffee–tree had the shortest growth period, ten weeks. It made 90 percent of its growth in 36 days from May 9th to June 14th.

Sugar maple grew for about 17 weeks with 90 percent of its growth occurring in 75 days from May 9th to July 23rd. These data differ from those of Kienholz (1941) who reported this species to make 90 percent of its growth in Connecticut from about May 10th to June 10th. Reimer (1949) reported a seven-week growing season in Indiana from April 14th to May 26th, and Cook (1941) reported sugar maples in Rensselaer County, New York, to grow for 35 days from May 16th to June 20th.

Silver maple grew much more gradually, about 20 weeks; and took 80 days for 90 percent of its growth.

Chinese chestnut had an exceptionally long growing season and almost constant growth rate from May 12th to August 7th. Ninety percent of its growth occurred during 91 days.

Paper birch had the longest growing season. Its growth curve closely resembles that of sugar maple and witch–hazel. Paper birch started growing by April 19th and

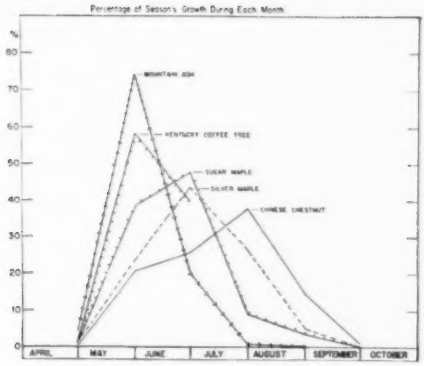

FIGURE 3. *Percentage of season's height growth added during each month for 5 deciduous species during 1954 at Westfield, Mass.*

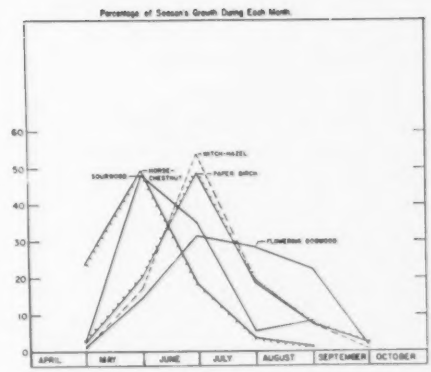

FIGURE 4. *Percentage of season's height growth added during each month for 5 deciduous species during 1954 at Westfield, Mass.*

continued to September 11th. Ninety percent of its growth took 98 days. Kienholz (1941) reported a shorter growing season in Connecticut for paper birch with 90 percent of growth occurring from May 20th to July 20th, and no growth occurring after mid-August. The growth pattern of witch–hazel was similar to that of paper birch and silver maple. It grew for 18 weeks and put on 90 percent of its growth in 84 days from May 15th to August 7th. Like sourwood, it manifested a slight resurgence in August after a mid-July lull. Nevertheless, its total growth in July exceeded that in August.

Flowering dogwood showed a growth pattern unlike that of any other species. It had a particularly long growing season. Its most rapid growth occurred during the first week in August, but thereafter it slowed down suddenly, so that the total monthly growth of June and July exceeded the total monthly growth of August. Flowering dogwood grew from April 24th to September 4th, with 90 percent of growth occurring during 95 days from May 15th to August 18th. This species has been reported to grow all summer and to stop only temporarily during periods of adverse environmental conditions (Meyer and Anderson, 1952).

Most of the sourwood specimens had been severely winter–damaged and their tips killed back. They were therefore measured from the axil of the outermost surviving bud, which in each case produced a shoot that assumed the lead. Sourwood grew for about 18 weeks with 90 percent of its stem elongation occurring during 89 days from May 13th to August 10th. Thus considerable growth occurred after the average tree stopped growing. This was because of the unusually wide divergence of cessation dates from June 29th to September 14th. Some individual trees showed a growth resurgence just at the average date of cessation for the whole group. The percentagewise growth after the average terminal date was about 8 percent. Many of the trees bloomed, the inflorescence in some cases arising on the new leading shoot terminally and in other cases laterally or on a side branch.

Horse–chestnut grew for eighteen weeks and made 90 percent of its growth in 91 days from April 24th to July 24th. There was much variation among individual trees in this species, and one tree made 90 per-

cent of its growth in 65 days. Probably all growth of horse-chestnut after mid-June was merely bud elongation.

Percentage of season's growth during each month. Figures 3 and 4 show the amount of growth accomplished during each month of the growing season. Growth of mountain-ash, Kentucky coffee-tree, horse-chestnut and sourwood was characterized by a rapid spring acceleration. These species made their greatest growth in May. Sugar maple, silver maple, paper birch, and witch-hazel formed an intermediate group which started slowly and made the greatest growth in June. Thereafter, growth of this group slowed down considerably. Flowering dogwood and Chinese chestnut formed a third category which had conspicuously long growing seasons. Although June was a month of greatest growth for flowering dogwood, this species grew only slightly less in July and August. Flowering dogwood grew more in August, percentage-wise, than did any other species. However it slowed down rapidly thereafter. Sourwood grew slightly more in August than in July, thus showing a bimodal growth curve. The greatest percentage of growth during any one month was 74 percent which was made by mountain-ash in May.

Discussion

The present study reinforces earlier emphasis on the individuality of seasonal growth patterns for different species of forest trees and suggests that some species are more dependent on stored foods than others for height growth. Despite the fact that all trees were grown with considerable spacing and in soil of high fertility there was pronounced variation in growth behavior of different species. The growing season lasted only ten weeks for some species but twice as long for others. Some species like mountain-ash made a sudden burst of growth in the spring and completed most height growth in less than a fourth of the frost-free season. Some species had growing seasons of intermediate length while others like Chinese chestnut and dogwood started slowly and continued to grow during a large part of the summer.

All species began to grow before the threat of frost was over and, despite the high level of soil fertility in this experiment all of them completed most of their growth long before the frost-free season ended. In an average frost-free season in Westfield, Massachusetts, which runs from the beginning of May to mid-October, a total of 166 days, 95 percent of the growth of paper birch, which had the longest growing season, was already completed by August 18th. One species, mountain-ash, had already completed 95 percent of its growth as early as June 9th. Kramer (1943) has pointed out that growing seasons of some trees may quantitatively equal the frost-free season and this is so only because these trees stop growing before frost begins in the fall and start growing before frost ceases in the spring. It has been generally held that deciduous trees make their height growth at the expense of prior-year photosynthate rather than products of current photosynthesis (Büsgen and Münch 1931; Loomis, 1935). This is so because in some species much height growth occurs early in the spring before an effective photosynthetic mechanism has developed. Such trees stop growing some time during the summer when the leaves are carrying on photosynthesis very effectively. Presumably carbohydrates are then accumulated during the rest of the summer. Carbohydrate reserves in many deciduous trees are at a minimum in early summer and build up to an autumn peak (Jones and Bradlee, 1933; Siminovitch, *et al.*, 1953; Kozlowski, 1955). It appears likely, however, that there are some basic differences in deciduous trees with regard to the relative amount of prior-year and current-year photosynthate that is utilized in height growth. A tree like mountain-ash which completes most of its height growth early depends primarily on carbohydrate manufactured during the previous year. Flowering dogwood which continues to grow all

summer may well begin growth using stored carbohydratest and sometime later may gradually utilize more products of current photosynthesis for height growth.

Apparently the shapes of growth curves of some species can be altered only to a limited extent even by severe changes of climate within the natural ranges of trees. Yellow poplar, for instance, distributes its growth over four to five months in North Carolina, whereas in Pennsylvania it makes most of its growth within a two-month period. In North Carolina, yellow poplar made about one-fifth of its total growth during April. In each of the next three months however it made about as much growth as it made in April (Kramer, 1943). Much of the April growth was undoubtedly made at the expense of stored foods and, if carbohydrate reserves were rapidly depleted in spring as most carbohydrate cycles in deciduous trees seem to show, then a considerable part of the later mid-summer growth was presumably made with products of current photosynthesis. In Pennsylvania yellow poplar made almost half its growth in May, presumably at the expense of stored foods. Most of the rest of total growth was made in June, slightly less than 40 percent, and some of this may have been made at the expense of products of current photosynthesis. The fact that a much longer percentage of the total seasonal growth of yellow poplar occurred during the first month in Pennsylvania than during the first month in North Carolina indicates that, in the northern part of its range, the yellow poplar depends on stored foods more than it does in the southern part. The first month's growth is likely to be made largely with prior-year photosynthate since considerable elongation occurs before leaves are fully expanded and before the tree has attained maximum photosynthetic capacity.

Shapes of growth curves of some species are altered much less than is that of yellow poplar in different parts of the natural range. The growth of white ash in North Carolina was compared with growth of the same species in Connecticut and the peak was shown in both curves. Mountain-ash did however have a somewhat longer growing season in North Carolina than in Connecticut (Kramer, 1943). It has also been shown that the shapes of growth curves of conifers in different parts in their natural ranges are very similar. Growth curves of red and white pine were similar in New Hampshire and in North Carolina (Kienholz, 1934; Kramer, 1933). The North Carolina climate merely increased the absolute lengths of the growing seasons of white and red pine but did not change the relative lengths nor the shapes of their growth curves. It thus appears that some species tend to utilize only stored carbohydrates for height growth and have a characteristically short growing season even in the southern parts of their ranges. Further experiments performed on species with characteristically short and long growing seasons, like mountain-ash and flowering dogwood, to determine the amounts of carbohydrate reserves accumulated by late fall may be helpful in enhancing knowledge of tree growth. Information is needed on the amounts of food used at various times of the year in height growth. The ability of a species to make an early growth using carbohydrates may be a significant factor in its competition with other species which tend to deplete their carbohydrates slowly during most of the frost-free season and thereby leave little accumulated reserve for the following year.

The authors acknowledge the cooperation of Mr. Lester Needham of Adams Nursery, Westfield, Massachusetts, whose courtesies made this study possible.

Summary

1. Ten deciduous tree species were measured for height growth at approximately weekly intervals in a nursery in Westfield, Massachusetts, during the growing season of 1954. Marked species differences occurred in seasonal growth patterns.

2. Mountain–ash made the most rapid early growth and completed 95 percent of its growth by June 5th. Kentucky coffee–tree made a slower start and finished all growth before the end of June. Horse–chestnut had a growth pattern similar to mountain–ash and quantitatively grew very little. Chinese chestnut and flowering dogwood made very slow starts and then grew at a nearly constant rate during June, July, and part of August. Sugar maple, silver maple, paper birch and witch-hazel were intermediate in their growth characteristics between the above two groups.

3. Mountain–ash, Kentucky coffee–tree, horse–chestnut and sourwood grew more in May than in any other month. Sugar maple, witch-hazel, and paper birch showed a maximum of growth in June, Chinese chestnut in July, while flowering dogwood grew almost equally in June, July and August.

4. The length of the period during which the middle 90 percent of growth occurred was as follows: paper birch, 98 days; flowering dogwood, 95 days; Chinese chestnut and horse–chestnut, 91 days; sourwood, 89 days; witch–hazel, 84 days; silver maple, 80 days; sugar maple, 75 days; mountain–ash, 39 days; and Kentucky coffee–tree, 36 days.

5. All trees started growth in the spring before danger of frost left and stopped growing in the summer usually long before fall frosts began.

6. Differences in seasonal growth patterns suggest that some species with short growing seasons use only prior-year photosynthate for height growth while species with long growing seasons use prior–year carbohydrate early in the spring and may utilize current–year photosynthate for height growth later in the summer.

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Canker and Dieback of Poplars Caused by Dothichiza Populea

BY
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CANKER OF POPLARS, caused by *Dothichiza populea* Sacc & Br., has been known in the United States since 1915, particularly in the Central and Eastern States. The fungus attacks young trees in nurseries and plantations, but has not been found on trees growing naturally in the forest. Its importance, therefore, lies in the extensive damage that occurs occasionally on plantation trees. Frequently it attacks only twigs and small branches, causing a limited amount of dieback; and its presence may be overlooked until weather or environmental conditions become particularly favorable for its spread.

Because of the increased interest in the selection and breeding of native, exotic, and hybrid poplars, a brief study has been made of the disease caused by *Dothichiza populea* in this country, especially in relation to the susceptibility of hybrid poplars. This report describes the distribution and symptoms of the disease, the causal organism, the results of inoculations of hybrid poplar clones, and the comparative susceptibility of the clones.

Hosts and Distribution

In the United States, *Dothichiza populea* was first reported in 1916 by Hedgcock and Hunt (1916) as the cause of a disease of Lombardy poplar, *Populus nigra italica Muenchh.*[1] Hedgcock (1927) found that the range of *D. populea* extended from Maine to Virginia and westward to Minnesota, Nebraska, and New Mexico, and that the following species of poplar were susceptible: *P. brevifolia* Carr., *P. deltoides* Marsh., *P. canadensis* Muenchh., *P. eugenei* Simon-Louis, *P. petrowskyana* Schroed., *P. simonii* Carr., *P. simonii fastigiata* Schneid.

The fungus was reported in Massachusetts by W. H. Davis (1935) as the cause of dieback on *P. alba pyramidalis* Bunge. Detmers (1923) described it on Norway or Carolina poplar (*P. eugenei*), causing extensive injury and death of young plantation trees in Ohio. More recently S. H. Davis (1942) reported the susceptibility of these additional hosts in Pennsylvania: *P. acuminata* Rydb., *P. berolinensis* Dipp., *P. nigra betulifolia* Torr., *P. sargentii* Dode, and *P. suaveolens* Fisch. The disease also occurs on Lombardy poplar in Ontario (Moss 1922) and New Brunswick (Güssow 1917), Canada.

In Europe, *Dothichiza populea* has been recognized as an important pathogen of poplars since 1903 (Delacroix). Goida-

[1]Authorities for most of the names of species and varieties of poplars are from Rehder's "Manual of Cultivated Trees and Shrubs," 2nd ed., 1940.

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nich (1940) summarized the range of the disease as follows: Italy, Switzerland, France, Belgium, Holland, England, Germany, and Romania. Natural infection by the fungus has been reported in these countries on a number of poplar species, varieties, and hybrids, principally in the Tacamahaca and Aegeiros groups.

Van Vloten (1938) tested by inoculation the susceptibility of the poplars most commonly grown in Holland, or used experimentally, with the following results:

Resistant: *P. fremontii* Wats., *P. brabantica* Houtz., *P. marilandica* Bosc., *P. eugenei*, *P. regenerata* Henry, *P. regenerata erecta* Houtz., *P. serotina erecta* (Selys) Henry.

Moderately resistant: *P. nigra italica*, *P. serotina* Hartig, *P. gelrica* Houtz., *P. trichocarpa* Torr. & Gray, *P. candicans* Ait.

Moderately susceptible: *P. nigra plantierensis* Schneid., *P. charkoviensis* Schroed., *P. Lloydii* Henry, *P. Wislizenii* Sarg., *P. nigra typica* L., *P. nigra betulifolia*, *P. berolimensis*, *P koreana* Rehd.

Susceptible: *P. tristis* Fisch., *P. laurifolia* Ledeb., *P. tacamahaca* Mill., *P. suaveolens*, *P. rasumowskyana* Schroed.

He found that, in *P. deltoides missouriensis* Henry (*P. angulata*, Ait.), and *P. robusta* Schneid., the degree of susceptibility varied among individual trees. From the results of his inoculations he concluded that species of the Tacamahaca group were more susceptible than those in the Aegeiros group, but none of the species available for testing was immune.

Dothichiza populea has been reported only once on quaking aspen (*P. tremuloides* Michx.) and large-toothed aspen (*P. grandidentata* Michx.) in the United States (Honey 1944). No report of its occurrence on the European aspen (*P. tremula* L.) has been found in literature.

Symptoms

Dieback of small stems or shoots frequently results from girdling cankers caused by *Dothichiza populea*. Cushion-like fruiting bodies are formed on the dead or wilting portions. The fungus may infect through bark at the base of small lateral twigs and spread from such twigs into a stem or branch, on which a lesion or canker then develops around the base of the twig (Fig. 1). Similar cankers form around injured buds. Cankers of this type and the fruiting bodies on the cankers are the earliest and most important diagnostic symptoms.

The development of cankers on branches or stems varies to a considerable extent in relation to the host reaction. On young fastigiate trees and those with numerous small upright branches, the cankers may girdle the branches rapidly, causing pronounced dieback. The fungus may then grow downward into the main trunk, forming brown necrotic areas in the bark. As these infected areas increase in size, the bark becomes cracked at the center and margins, and considerable callus may form.

If such cankers are produced in the upper part of the trunk, dieback of the entire crown results. On poplars with large out-

FIGURE 1. *Canker caused by* Dothichiza populea *on Volga poplar.*

spreading branches, and those resistant to the fungus, small branch cankers with smooth brown bark, callused at the margins, usually increase in size very slowly, causing no dieback or other appreciable injury. More extensive cankers, however, may be formed on stems of poplars that have numerous small lateral twigs along the stem. Infection from such twigs may spread rapidly into the stem, forming cankers with yellow or brown depressed bark, and abundant fruiting bodies. As the canker develops, the bark cracks and extensive callus is produced. This tends to hinder the further spread of the fungus.

On hybrid poplars, cankers of various types may occur on one tree, and some may resemble those caused by other parasitic fungi. A diagnosis is then extremely difficult unless fruiting bodies are present or the causal organism is isolated in culture.

The Causal Fungus

Dothichiza populea was first described by Saccardo (1884) and Briard in 1884 on dead branches of Populus species in France. In 1903 Delacroix reported it as a serious parasite of poplar in France and described the symptoms of the disease. Klebahn (1933) studied the morphology of the fungus and concluded that its characteristics did not correspond with those of the genus *Dothichiza*. He therefore established a new genus *Chondroplea*, naming the poplar fungus *C. populea*, with synonyms *D. populea*, *Cytosporella populea* Ord., and *Dothiorella populea* Sacc. (1937). Certain European investigators, particularly Goidanich (1940), have adopted Klebahn's designation, while Van Vloten (1938) prefers to retain the name *Dothichiza populea*, since he believes that Klebahn's interpretation of spore-formation is incomplete. In American literature, the fungus is still designated as *D. populea*.

On specimens of cankered poplars examined in the author's study, the fruiting bodies formed small subepidermal spherical cushions of mycelium, about ½ to 2mm. in diameter. As they matured and developed into pycnidia, the bark became ruptured, and the pycnidia opened irregularly and widely, exposing the fruiting layer. This layer was composed of densely compact slender condiophores, simple and continuous, or occasionally branched and septate, straight or very slightly curved, tapering at the tips, on which the conidia developed singly. The conidia were unicellular, hyaline, ovate-piriform or spherical, 9-13 x 7-9μ.

The conidia were produced in abundance and filled the pycnidial cavity. When mature, and when moisture conditions were favorable, the spores were extruded in a broad olive-buff cirrhus or in mass, and collected on the surface of the bark around the pycnidium. A pycnidium seemed to produce spores for a relatively short time and thereafter the conidiophores disappeared.

During the summer many such pycnidia still contained the unextruded spores most recently developed, but no conidiophores were found. The bark through which the spores extruded broke away, exposing the dark brown or black wall of the empty pycnidium, and giving the appearance of a small cup-like body sunken in the bark. New pycnidia were formed as the dieback or canker progressed, so that mature spores were present throughout the summer and autumn.

Dothichiza populea apparently overwinters by spores in late-developing unopened pycnidia, and by mycelium within the bark tissue. In the spring, new pycnidia may appear on the stems killed or weakened the previous year and on cankers resulting from infection of the preceding season.

In the United States, no ascogenous or perfect stage of the fungus is known. In Italy, Voglino (1911) found *Cenangium populneum* (Pers.) Rehm associated with *Dothichiza populea* and reported experiments by which he attempted to prove that the latter fungus was the imperfect form

of the Cenangium species. Other investigations, particularly by Klebahn (1933), Van Vloten (1938), and Gremmen (1952), who compared the two fungi on the hosts and in culture, tend to disprove this relationship.

Specimens of *Cenangium populneum* have been collected from various localities in the United States, usually on dead branches of the aspens, *Populus tremuloides* and *P. grandidentata,* and occasionally on stems of hybrid poplars that have been killed by *Septoria musiva* Pk. (Waterman 1954). In this study, monoascospore cultures of *C. populneum* from *P. tremuloides* and from clones of hybrid poplars, *P. maximowiczii* Henry × *P. berolinensis,* and *P. maximowiczii* × *P. caudina* Ten., were compared with monoconidial cultures of *D. populea* from a clone of the hybrid poplar *P. petrowskyana* × *P. caudina.*

Dissimilar colonies were produced, as shown in Figure 2. The growth periods for both of these monospore isolates were identical. The conidial isolations formed typical pycnidia of *D. populea,* but no pycnidia developed in the ascospore isolations. Inoculations with the isolates of *C. populneum* were made on several clones of hybrid poplars, but no infection occurred. The results will be discussed later, in relation to the inoculations with *D. populea.*

Susceptibility of Poplar Species and Hybrids

The large number of species of poplar reported in literature as susceptible to *Dothichiza populea* under natural conditions suggests that hybrids of these species might be susceptible. To determine whether there are clonal variations in susceptibility among hybrids, 92 clones representing 38 hybrids were tested by inoculations.

These clones were selected from the collection of hybrids developed by the Northeastern Forest Experiment Station of the U. S. Forest Service. The species or variety names given in Table 1 are those by which the parent trees were originally designated (Schreiner 1937). Experimental plots for testing disease susceptibility were established at Cheshire, Conn., and Williamstown, Mass. Observations of natural infection on hybrids and species of poplar in the Northeastern and North Central States were also made.

Inoculations.—All inoculations were made during the summer on shoots of the cur-

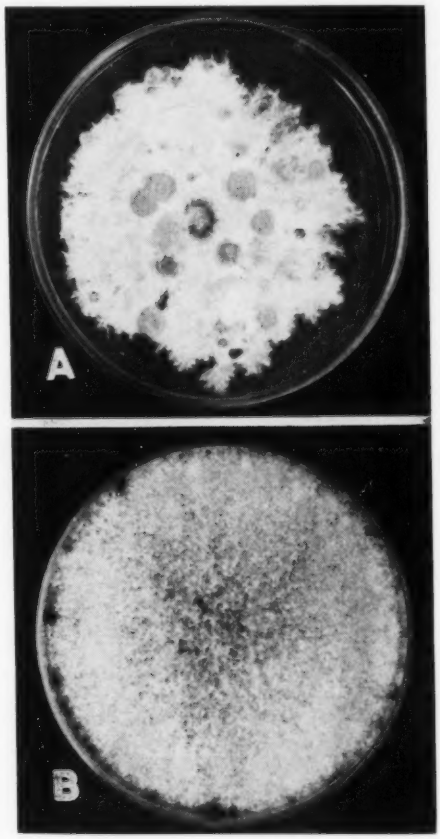

FIGURE 2. A, *monoconidial culture of* Dothichiza populea,, *with immature pycnidia.* B, *monoascospore culture of* Cenangium populneum. *Length of growth period for both isolates was identical.*

rent season's growth from unrooted cuttings or from stumps of young nursery trees that had been cut back at the end of the previous growing season. The inoculum was mycelium from non-sporulating cultures on malt agar, or a water suspension of spores from cankers that had been stored over winter in a refrigerator at 40°F.

Inoculations were made in wounds on the young shoots. Two sides of a triangular piece of bark were cut with a sterile scalpel. The piece of bark was turned back from the stem sufficiently to allow the insertion of a small piece of agar with mycelium, or of a few drops of water suspension with spores. The bark was then pressed back against the inoculum and the inoculated part of the stem was wrapped with wet cotton and waxed paper. One control on each inoculated clone was made by cutting the bark as described, inserting a small block of sterile agar, and wrapping with wet cotton and waxed paper. The wrappings on all inoculated stems and controls were removed after 48 hours.

In July 1950, 51 clones of hybrid poplars in the experimental plot at Cheshire, Conn., were inoculated. Four inoculations per clone were made with mycelium from monospore cultures, and one inoculation with a spore suspension. At Williamstown, Mass., in August 1951, 3 of these same clones and 41 additional clones were inoculated with mycelium from monospore cultures, with 3 inoculations per clone. All of these latter clones had proved to be resistant to the canker-producing fungus, *Septoria musiva* (Waterman 1954), when tested by inoculations.

During the growing season in which the inoculations were made, no evidence of infection was found. In most cases, the inoculation wounds seemed to heal, as did the wounds on the control trees. In the following spring, however, when the new growth began to develop, sunken bark around the inoculated areas indicated that the stems had become infected.

On the stems of fastigiate trees, girdling cankers and dieback occurred during the growing season. *Dothichiza* fruiting bodies developed in abundance around the inoculation wounds. On other clones, infection produced cankers with depressed bark and cracked margins, sometimes with a few fruiting bodies. Occasionally the fungus did not fruit on the cankers, and heavy callus around the infection area prevented the further development of the canker. Infection from inoculations with spores was identical with that from inoculations with mycelium.

The susceptibility of the clones was rated according to the host reaction to infection as indicated by the results from the inoculations. All inoculated stems were collected 2 years after inoculation. Each inoculation was tallied into one of the following classes: Class 1, wound healed, no canker or dieback; Class 2, small canker around the inoculation wound, but healed with callus; Class 3, canker with cracked and callused margins, usually with *Dothichiza* pycnidia, wood exposed; Class 4, girdling canker with pycnidia, dieback. From the tally, an average was obtained for each clone and this was used as the basis for rating susceptibility. A rating of 1.0 indicated no infection; a rating of 3.1 to 4.0, high susceptibility.

Table 1 gives the susceptibility ratings of the clones, according to parentage, to indicate variations in susceptibility among clones from each cross combination. Most of the clones with *Populus deltoides* as one of the parents were uninfected, or only slightly susceptible. Seven clones in which *P. maximowiczii* was the female parent were rated as slightly susceptible.

However, the low susceptibility ratings for the clones with this female parent are questionable so far as susceptibility to *Dothichiza populea* is concerned. These hybrids are highly susceptible to stem infection by *Septoria musiva* (Waterman 1954), which was abundant in the experimental plot. The shoots inoculated with *D. populea* became infected with *S. musiva*, and some

TABLE 1. Susceptibility of hybrid poplar clones to Dothichiza populea, *based on type of infection resulting from inoculations.*

Parentage of Populus hybrids (female listed first)	No infection	Susceptibility[1] Slight	Moderate	High
	No.	*No.*	*No.*	*No.*
angulata × berolinensis	----	----	2	1
angulata × deltoides	1	----	----	----
angulata × incrassata	----	----	2	----
angulata × nigra plantierensis	----	----	2	----
angulata × volga	----	----	----	2
angulata × unidentified cottonwood	1	----	----	----
candicans × berolinensis	----	----	1	1
charkoviensis × berolinensis	----	----	----	2
charkoviensis × caudina	----	----	2	7
charkoviensis × deltoides	----	----	1	4
charkoviensis × incrassata	----	----	----	3
charkoviensis × nigra plantierensis	----	----	----	4
charkoviensis × robusta	----	----	----	1
charkoviensis × trichocarpa	----	----	2	----
charkoviensis × volga	----	----	----	1
charkoviensis × unidentified cottonwood	----	----	----	2
deltoides × berolinensis	----	1	----	----
deltoides × caudina	----	1	2	----
deltoides × grandidentata	----	1	----	----
deltoides × trichocarpa	1	2	----	----
deltoides × volga	----	1	3	----
maximowiczii × berolinensis	----	3	4	1
maximowiczii × caudina	----	1	----	----
maximowiczii × nigra plantierensis	----	2	----	----
maximowiczii × trichocarpa	----	1	----	----
nigra × laurifolia	----	----	6	1
nigra × nigra italica	----	----	----	1
nigra × trichocarpa	----	----	1	1
nigra baatanicorum vitrum × trichocarpa	----	----	1	----
nigra baatanicorum vitrum × volga	----	----	1	----
nigra betulifolia × trichocarpa	----	----	1	----
petrowskyana × caudina	----	----	3	1
rasumowskyana × caudina	----	----	1	----
rasumowskyana × nigra plantierensis	----	----	----	1
sargentii × berolinensis rossica	----	1	2	----
sargentii × nigra italica	----	----	1	----
sargentii × sargentii	----	----	----	1
sargentii × simonii	----	----	----	1
sargentii × berolinensis	----	----	1	----

[1]Classes of susceptibility were derived from averages of individual clones obtained by multiplying the number of individual inoculations tallied into a class by the class number and dividing the sum of the products of all classes by the total number of inoculations in the clone. Average 1.0, no infection; 1.1-2.0, slight susceptibility; 2.1-3.0, moderate susceptibility; 3.1-4.0, high susceptibility.

of them were killed by that fungus within a year. On the shoots of the clones rated as slightly susceptible, the inoculation wounds had healed or had formed only small cankers with excessive callus. Definite cankers around the inoculation wounds occurred on the stems of the remaining clones and in some cases girdled the stems before the infection by *S. musiva* became serious.

Of the remaining clones of other hybrids, 39 were moderately susceptible and 36 highly susceptible. Some of these trees also became slightly infected by *Septoria musiva*, but the results of the Dothichiza inoculations were sufficiently distinctive to permit a rating of susceptibility. On many of the cankers, pycnidia of *D. populea* were abundant and the cankers continued to develop during the second growing season. On the highly susceptible fastigiate trees with *Populus charkoviensis* as the female parent, the infection spread into the side branches during the second season. No natural infection, however, could be found in any trees in the experimental plot.

Inoculations with Cenangium populneum. —In Voglino's study of the relation between *Cenangium populneum* and *Dothichiza populea* (1911), he reported that he inoculated wounds on trunks of 2-year-old poplars with a water suspension of the Cenangium spores. From one inoculation he obtained a small lesion with fruiting bodies resembling those of *D. populea*. His description is not exact enough to prove that his results were positive.

In the present study, 1- and 2-year-old stems of 18 hybrid poplar clones in the plot at Cheshire, Conn., were inoculated in June 1953 with mycelium of the isolates of *Cenangium populneum* previously mentioned. The method of inoculation was identical with that used in the Dothichiza inoculations. The clones were those that had proved to be susceptible to *Dothichiza* by inoculation, as follows: *Populus nigra* × *P. laurifolia*, *P. nigra* × *P. trichocarpa*, *P. maximowiczii* × *P. berolinensis*, *P. maximowiczii* × *P. trichocarpa*, *P. charkoviensis* × *P. berolinensis*, *P. charkoviensis* × *P. caudina*, *P. charkoviensis* × *P. deltoides*, *P. charkoviensis* × *P. incrassata*, *P. charkoviensis* × *P. nigra plantierensis*.

The inoculated stems were examined after 1 and 2 years of growth, but no dieback or cankers were present. The inoculation wounds healed, and cultures from the wound tissue did not produce the *Cenangium*. These results indicated, therefore, that *C. populneum* did not infect the bark and wood of the living trees.

Natural infection by Dothichiza populea. On trees of hybrid clones in plantations at Williamstown, Mass., other than the one used for inoculations, a few Dothichiza cankers were present, particularly on trees of clones with *Populus charkoviensis* as the female parent. Infection caused girdling cankers on fastigiate branches or dieback of small lateral twigs. Cankers with smooth slightly raised bark developed around the bases of these twigs, but no extensive injury to the larger stems or branches resulted.

Young trees in plantations of selected clones of hybrids and species of poplars at Madison, Wis., and Rochester, Minn., showed slight infection, with branch cankers. In the plantings at Rochester, girdling cankers and dieback occurred on *Populus nigra italica*, *P. deltoides*, *P. robusta*, *P. petrowskyana*, *P. tristis*, *P. charkoviensis*, Volga poplar, and the hybrids *P. charkoviensis* × *P. caudina*, *P. charkoviensis* × *P. deltoides*, *P. berolinensis* × Northwest poplar, Russian poplar × *P. tacamahaca*. Pynidia usually were abundant on branches that had been killed back. From cankers without pycnidia, *D. populea* was isolated in culture.

Discussion

The wide host range of *Dothichiza populea*, reported in American and European literature, and the results of the inocula-

tions in the present study, emphasize the susceptibility of species and hybrids of poplar in the Tacamahaca and Aegieros groups. The degree of susceptibility varies among the clones of species and hybrids, and the resulting injury is somewhat dependent upon the type of growth of the trees. Fastigiate branches or small stems may be girdled and die back. Trees with numerous lateral twigs may develop small cankers at the base of such infected twigs. These cankers may develop perennially into large trunk cankers with conspicuous callus and exposed wood.

In the inoculation experiments, made in July and August, no infection was evident until the following spring, when the trees began to put out new growth. This delay in visible evidence of infection has been reported also by Schönhar (1955). This indicates that natural infection of twigs or branches may take place in the summer when the spores are discharged from the pycnidia, but the results of such infection will not be evident until the following growing season.

In the United States, the disease has never been of sufficient importance to require a detailed study of control measures. Occasionally a plantation may be severely attacked in a particular locality, but the disease in general continues only in a mild form with no serious injury.

In Europe, however, *Dothichiza populea* is considered to be one of the most dangerous parasites of poplar, especially of young or newly planted trees, or trees that have been weakened by other factors. Goidanich (1940), in describing these factors, mentions low spring temperatures, transplanting in the autumn, poor drainage, drought, wounding by pruning or by soil cultivation, and infertile soil. Although the disease seems to be endemic in the United States, the potentialities of the fungus as a parasite warrant particular care in the selection of disease-free stock for planting, and in providing the best possible growing conditions for young plantation trees.

So far as known, *Dothichiza populea* has only the one fruiting stage on branches and stems. No related fruiting stage has ever been observed on the leaves. Hedgcock (1927) reported the artificial infection of poplar leaves by spraying with a spore suspension. Schönhar (1953), however, obtained negative results from inoculation of poplar leaves.

The spread of the fungus, therefore, is by means of spores from the pycnidia on twigs or cankers. Rain, wind, and insects are probably the carriers. Pycnidia may be formed in abundance on cankers, dead twigs, or branches, and large masses of spores exude from the pycnidia. However, on many small branch cankers and on slightly susceptible hosts, no pycnidia are produced and the presence of the causal organism is determined only by culturing the canker tissue. Apparently the fungus, in this country, rarely builds up inoculum in sufficient quantity for the disease to reach epidemic proportions under conditions favorable for its spread.

Summary

Dothichiza populea has been known in the United States since 1915 as a canker-producing parasite on young plantation trees of poplar, particularly *Populus nigra italica*. It occasionally causes extensive loss, but has not been found on natural growth of poplars in the forest. It infects a wide range of Populus species, especially those in the Tacamahaca and Aegieros groups. In Europe it is considered an important pathogen of poplars. Cankers are formed on branches or trunks, sometimes girdling the infected part and causing dieback. Pycnidia of *D. populea* occur on cankers or on dead twigs or branches. No other fruiting stage is known.

Inoculations of 92 clones representing 38 hybrid poplars, with black or balsam poplars and cottonwoods as parents, showed that 75 clones were moderately or highly suceptible. *Cenangium populneum*, which

has been reported in Europe as the perfect stage of *Dothichiza populea*, was inoculated into stems of selected clones, but no infection occurred. Cultures also failed to prove any relationship between the two fungi. In a plantation of selected clones of hybrids and species of poplar, branch and stem cankers from natural infection by *D. populea* were found on *P. nigra italica*, *P. deltoides*, *P. robusta*, *P. petrowskyana*, *P. tristis*, *P. charkoviensis*, Volga poplar, *P. charkoviensis* × *P. caudina*, and *P. charkoviensis* × *P. deltoides*.

The disease has not been sufficiently severe in the United States to warrant a detailed study of control measures. Because of the possibility of infection among plantation trees, however, care should be taken to obtain disease-free stock for planting, and to maintain the best possible growing conditions in a plantation.

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Studies of Regeneration in Forest Stands Devastated by the Spruce Budworm

I. Evidence of Trends in Forest Succession During the First Decade Following Budworm Devastation.

BY
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FOR MANY YEARS the problems presented by changes in forest composition following major disturbances such as cutting, fire, and insect outbreaks, have commanded the attention of foresters and forest entomolgists. It is a common observation that forest stands may change both in stocking and in species composition following such disturbances. These changes are of great theoretical interest since they cast considerable light on the growth habits and competitive vigour of the various tree species entering the forest succession; they are at the same time of profound economic and social significance since they affect the nature and productivity of future wood-using industries in the devastated areas.

Throughout the first half of this century, and during recent decades in particular, the spruce budworm, *Choristoneura fumiferana* Clem., has destroyed large tracts of spruce-balsam fir forest in northern and northeastern North America. Some entomologists have been inclined to attribute the severe outbreaks of recent decades to the selective cutting practices of the past, suggesting that these have favoured the development of large tracts of balsam fir, *Abies balsamea* (L.) Mill. Graham (1939) expressed this view in relation to the spruce budworm outbreaks that devastated the spruce - balsam stands of eastern United States and Canada between 1909 and 1920. Of these outbreaks he wrote:

> "All the available evidence appears to prove that this great series of outbreaks . . . arose as a result of the type of forest developed in the infested region by a combination of unregulated, or improperly regulated, cutting operations, forest fires, and natural succession. These agencies produced a forest that contained a very high percentage of balsam fir, the most suitable food tree of the spruce budworm."

From the work of Blais (1954) however, and from consideration of the nature of the Canadian boreal forest, it is probable that severe outbreaks of the spruce budworm have occurred in the Canadian forest for many centuries. As a conclusion to his evidence that a widespread and destructive spruce budworm outbreak occurred in the latter half of the nineteenth century in the Sioux Lookout area of northwestern Ontario, Blais wrote:

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"Since the forests in this area had never been subjected to exploitation, all changes in the forest composition and all related phenomena are entirely natural. Spruce budworm outbreaks therefore appear to be a phase in the natural cycle of events associated with the maturing of balsam fir."

The observations of Graham and Blais suggest that the extensive exploitation of valuable pines and hardwoods in the east may have produced, artificially, the same predominance of balsam fir that follows in the natural course of succession in the northern boreal forest. In any event it is now universally recognized that a large tract of mature balsam fir, however brought about, is the essential precondition for a severe outbreak of the spruce budworm.

The widespread and repeated destruction of spruce - balsam fir forests by the spruce budworm has prompted speculation on the role of this insect in forest succession. Budworm outbreaks have destroyed many stands actually or potentially available for utilization by the pulp and paper industry, and this industry has tended in the past to value mixed stands of spruce and balsam fir in relation to their content of spruce. Although this tendency has become less evident in recent years, speculation on the role of the spruce budworm in forest succession still centers on possible changes in the proportions of spruce and balsam fir in succeeding stands. "Spruce" in this context refers primarily to budworm – susceptible white spruce, *Picea glauca* (Moench) Voss, although the less-susceptible black spruce, *P. mariana* (Mill.) B.S.P., often contributes substantially to the basal area of budworm-damaged stands and must be included in any discussion of post-budworm succession.

An early theory held that since balsam fir was regularly the most heavily damaged component of mixed spruce - fir stands, it must logically decrease following a budworm outbreak. This theory was recorded by Craighead (1924):

". . . . we usually find after the first 100 to 125 years [after fire] considerably more balsam. Such conditions are ideal for a budworm epidemic which appears and destroys a much higher percentage of balsam than spruce. The older the stand the more severe and selective the balsam thinning. Spruce has much better recuperative powers both from natural suppression and from budworm defoliation, consequently a larger number of spruce fill the gaps left by the balsam. The intensity of this conversion to pure spruce varies directly with the original percentage of balsam as well as with the age of the stand. . . . It is therefore logical to assume that the budworm plays an important role in the rotation of these trees and in the conversion of mixed spruce-balsam stands into a pure spruce stand. . . . It is true that mixed spruce-balsam stands would in time develop into purer stands due to the shorter life of balsam and its lesser ability to recover from suppression yet there can be little doubt that the budworm accelerates this process and is a fundamental factor in its accomplishment."

In the next decade the opposite theory began to emerge, as is evident in the following quotation from Swaine (1933) in which he reports data provided by J. C. Veness of the Dominion Forest Service:

"During the last generation, lumbering, fires and insect outbreaks have resulted in augmenting to an enormous degree the original quantities of balsam fir, and this tree will have a very prominent place in the pulpwood industry of coming generations. In the forests of New Brunswick, for example, one effect of the spruce budworm outbreak was to increase the percentage of balsam fir from about 50% in the old stand which was killed to 85% in the young crop which is now growing up."

After the lapse of a further eleven years, de Gryse (1944) expressed a view in direct contrast to Craighead on all important points. From his wording, it seems probable that de Gryse was directing his comments against just that sort of attractive hypothesis that Craighead had expressed:

"It has been observed, over and over again, that after a budworm outbreak, the percentage of balsam in the new stand is considerably higher than it was in the old.

> The extraordinary accumulation of debris on the surface, while seriously hampering spruce regeneration, seems to offer no obstacle to the rooting of balsam. Root competition and competition for light causes further reduction of spruce that may become temporarily established. Generally speaking, the predominance of balsam is such as to reduce the possibility of its replacement by the residual spruce for several generations if not forever. Under absolutely normal conditions, it is conceivable that sooner or later—in some localities—a spruce climax might develop from such antecedents. When the spruce budworm, however, enters into the picture, all such hopes vanish. It is a conservative estimate—probably an understatement—to say that, in many regions, any forest containing over 30% of balsam is more than likely to succumb to budworm attack upon reaching maturity. When this happens, not only the balsam but the greater part of the spruce associated with it will be killed and the forest will enter a new and more advanced stage in the succession towards a balsam climax."

It is apparent that unlike Craighead, de Gryse considered spruce to have a lower degree of shade tolerance than balsam, and to be in general a weaker competitor. It is also evident that in speaking of the hampering effect upon spruce regeneration of the "extraordinary accumulation of debris on the surface" after a budworm outbreak, de Gryse assumed that the seedlings that grow into the next crop of trees originate *after* a budworm outbreak, another point around which some difference of opinion has hinged. Regeneration surveys designed to determine simply the presence or absence of sufficient seedlings to replace the devastated stands have provided little reliable data to resolve these controversies. By the time such surveys are made, established but long-suppressed seedlings have profited from several years of released growth and give the impression of being vigorous, fast-growing seedlings of recent origin. It is clearly of more than academic interest to know whether the bulk of the seedlings that replace a devastated forest originate before, during, or immediately after a spruce budworm outbreak, if we are to entertain the hope of someday managing our spruce-balsam forests so as to anticipate the spruce budworm.

From the foregoing quotations it is evident that there thas been a considerable need for data that would take the discussion out of the realm of speculation and place it upon a basis of observed events. In particular, there has been a need for data that might indicate whether there is anything inherently more favorable to balsam succession in a budworm disturbance than there is in a similarly catastrophic disturbance by fire or cutting. For these reasons, a series of investigations of tree regeneration in budworm devastated areas was initiated by the Forest Insect Laboratory in the late 1940's, in the hope that some of these problems might be clarified. Several brief accounts of the early development of these investigations (Prebble, 1948, 1949) have already appeared.

The Forest Insect Laboratory in Sault Ste. Marie, Ontario, maintains field stations in three areas of heavy budworm damage: at Laniel in the province of Quebec adjacent to the northeastern boundary of Ontario (47° 03′ N., 79° 16′ W.); at Black Sturgeon Lake in north-central Ontario north of Lake Superior 49° 18′ N., 88° 52′ W.); and at Cedar Lake in northwestern Ontario (50° 11′ N., 93° 12′ W.). By the late 1940's, forest stands in these areas had been or were being destroyed by the spruce budworm. At Cedar Lake and at Black Sturgeon Lake the spruce budworm populations probably reached outbreak proportions by 1939 or 1940. At Black Sturgeon Lake the population was at its peak between 1945 and 1947, but dropped abruptly in 1948 and 1949. By this time the area of heavy defoliation extended roughly 160 miles from east to west and 100 to 120 miles from north to south, completely surrounding Lake Nipigon (Belyea, 1952). At Cedar Lake high populations of budworm have continued to

the present time. In comparison with the Black Sturgeon outbreak, mortality of balsam fir at Cedar Lake has come about through more prolonged exposure to less intense defoliation. In this way the Cedar Lake outbreak has lagged several years behind the Black Sturgeon outbreak in the history of mortality and breakup of overstory balsam fir, although balsam mortality is now virtually complete on the regeneration plots in both areas. By 1952 the Cedar Lake outbreak had extended over an area roughly 180 miles from east to west, and from 100 to 140 miles from north to south (Blais, 1954). Continued defoliation during recent years has considerably extended this area, principally to the south and southeast (Sippell *et al.*, 1953, 1954, 1955). The budworm outbreak in the Laniel-Timagami area preceded the Cedar Lake and Black Sturgeon Lake outbreaks by at least two years. Although there was considerable variation from place to place, possibly because of the scattered nature of balsam fir stands in this area, the spruce budworm was present in the area at least as early as 1937 (C. E. Atwood, personal communication), reached its peak during 1941 and 1942 (Brown, 1941, 1942), and had largely subsided as an outbreak population by 1947 (Macdonald and Prebble, 1947).

Between 1948 and 1950, regeneration studies were initiated in these three areas. These studies have proceeded along the following lines:

(a) The establishment of permanent sample plots on which successional development following spruce budworm devastation could be followed through periodic re-examinations. Soil and site description studies were conducted at the time the plots were established.

(b) Immediate study of existing regeneration to determine its age and height-growth relations with respect to budworm outbreaks.

(c) A re-tally of the regeneration plots during the 1955 field season to provide a check on any short-term trends that might have developed in the forest succession.

(d) Studies of the influence of quadrat size on the apparent distribution of seedlings, and on the accuracy of population estimates obtained from the sampling procedures adopted, conducted in order to facilitate the evaluation and interpretation of the main body of data obtained in the study.

Data gathered during these studies will be presented in a series of three contributions, the first of which is the present paper. In this first paper, which serves to introduce the series, data on site description, vegetation, stand composition, and the numerical and relative abundance of balsam fir and spruce seedlings, are presented. This paper is directed towards the first of the major objectives of the project, the comparison of the ratio of spruce and balsam fir in the devastated stands and in the new stand that follows.

A second contribution will deal with the second of the major objectives of the project, the age and origin of the regeneration in relation to the spruce budworm infestation. This paper will present data on the age and height-growth of balsam fir seedlings, and related studies on seed supply in the overstory and damage to the regeneration by the spruce budworm. These studies were conducted most intensively at the Black Sturgeon Lake Field Station.

A third paper planned as an outcome of these studies will treat the statistical aspects of sampling populations of balsam fir and spruce seedlings. This will include consideration of the accuracy of the estimate of seedling numbers per acre in relation to sample size, the influence of quadrat size on the apparent distribution of the seedlings, and the relation between per cent stocking and number of seedlings per acre as measured on milacre quadrats. While a discussion of sampling technique might logically precede the results presented in the first two papers in the series, the material available for the third paper is of a sufficiently fundamental nature that it requires a more elaborate expansion than would be appropriate to a simple description of the sampling procedures employed.

From the nature of the study it will be

many years before final conclusions can be drawn concerning changes in the study areas. It is anticipated that data arising from future re-examinations of the regeneration plots may justify the publication of brief accounts summarizing whatever trends may develop, particularly with reference to declining numbers of stems as natural thinning progresses and to the relative mortality of presently established spruce and balsam fir seedlings.

The present paper represents the work of a considerable number of people, and it is possible to indicate in detail the contribution of only a few of these. The project was initiated under the guidance of M. L. Prebble in 1948. Soil and site description studies were conducted by D. A. Fraser, who was also responsible for the selection of study areas and for part of the earlier analysis of regeneration data. J. B. Thomas established the regeneration plots at Laniel, and conducted studies of sampling intensity which guided the work in the Black Sturgeon and Cedar Lake areas. Regeneration plots at Black Sturgeon Lake were established by E. B. Ayer, while those at Cedar Lake were established by J. R. Rooke, who also conducted studies of quadrat size in relation to the apparent distributions of tree seedlings. A. W. Ghent has been responsible for the 1955 re-tally of the three study areas, for studies of the age and height-growth of seedlings, for the analysis and assessment of the data, and for the final revision of the present manuscript.

Methods

Study plots were selected to give a representative cross-section of sites on which forest stands of high balsam fir content had been damaged by the spruce budworm. The uniformity of soil conditions throughout each plot was checked with a soil auger, and a soil pit was excavated at a point outside each plot where the auger survey indicated conditions to be representative. The three-digit classification of site proposed by Hills (1945, 1952) and discussed by Fraser (1954), which evaluates the site properties of ecoclimate, moisture regime, and pore pattern or permeability, was adopted to describe site conditions on the study plots.

Rectangular study plots averaging one acre in area were established in uniform forest stands. Each plot was divided into chain-square (tenth-acre) blocks, the overall dimensions of the plots being some combination of simple multiples of chains, such as 2×5, 3×3, or 3×4, depending in some instances on the limitations imposed by the shape of the particular forest stand. Several plots as small as 2×2 chains, and one as large as 4×4 chains, were used in special cases.

The milacre quadrat was adopted as the basic sampling unit for seedling counts. Studies of sampling accuracy indicated that a 10 percent sample, or ten milacre quadrats per tenth-acre block, reduced the standard error of the population estimate to within ±15 percent of the mean in most instances. Milacre quadrats were located at random, following a procedure which gave a stratified-random sample in which each tenth-acre block was restricted to the reception of 10 milacre quadrats. This procedure ensured that a 10 percent sample was obtained from each tenth-acre block, as well as from the plot as a whole. The milacre quadrat locations were predetermined on grid-paper maps of the plots, the co-ordinates of the milacres being assigned from two-digit random tables. No restriction was placed on random clumping of the milacre quadrats within or along adjacent edges of the tenth-acre blocks.

Figure 1 illustrates a typical plot layout resulting from the foregoing procedure. The distribution of milacre quadrats shown in this figure is characteristic of the study plots. Numbers from one to ten within the milacres indicate the order in which the locations of the quadrats were assigned from the random tables, a numbering system which was retained throughout the field work. The extent of clumping of milacre quadrats shown in this figure represents a slight and non-significant reduction

in clumping from that predicted by the appropriate binomial calculations for an unstratified random sample.

A common practice in forest tree regeneration surveys on disturbed sites is to classify the regeneration either as advanced growth or as seedlings, in so far as the seedlings appear to have originated before or after some disturbance such as fire or cutting. It is certainly questionable if any real accuracy can be obtained with such a classification in the time that can be devoted to each seedling encountered in a regeneration survey, and this method of classifying regeneration has been criticized for this reason by Hosie (1953). Since the determination of the relative incidence of seedlings originating before and after spruce budworm devastation was a major consideration in the initiation of this study, the assumption of ability to make this distinction without critical examination of each seedling was clearly inappropriate. To facilitate such studies of the age relations of seedlings, a system of ten height classes was adopted, in which the seedlings were tallied by 6-inch height classes between ground level and 18 inches, and by one foot height classes from 2 feet to 8 feet. This procedure permitted the later determination of seedling age distribution by height class and facilitated the task of analyzing the growth of regeneration between the 1950 and 1955 plot inspections. The very small proportion of the regeneration greater than 8 feet in height invariably had a measurable breast-height diameter, so that this division point between height and diameter classes was well chosen. A light pole on which the successive height classes were marked was carried in the field, so that each seedling encountered on the quadrats could be accurately assigned to its proper height class.

Site, Vegetation, and General Topography

The soil in the three study areas is comparatively shallow, and immediately underlain by Precambrian bedrock, reflecting the

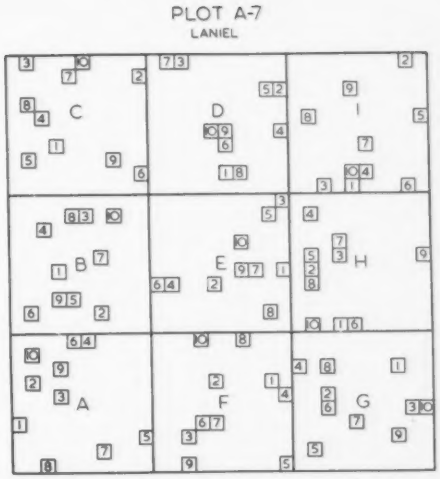

FIGURE 1. *Diagram of a 9/10 acre regeneration plot, typical of those established in this study. The distribution of milacre quadrats is characteristic of that obtained with the stratified-random method used in this study to determine quadrat locations.*

glaciation of Ontario within recent times. Small areas of exposed bedrock occur on some of the study plots. The uneven nature of this bedrock topography contributes to the complexity and distribution of the glacial drift. Thus the parent material of the soils may have diverse fabric, texture, and structure, factors that greatly influence the porosity, water-holding capacity, and nutrient levels of the soils, which are, in turn, reflected in the site quality.

Vegetation and site data for the 26 study plots are summarized in Table 1. The 3-digit site rating (Hills, 1952) indicates in order the values assigned to ecoclimate, moisture regime, and pore pattern. For space considerations, potential plant indicators have been assigned alphabetic symbols to which a key is given at the bottom of the table. Data on "trees per acre" indicate the number of stems greater than 1 inch in diameter. Total basal area of all tree species is given as a measure of the relative productivity of the various sites. The relative consequence of each of the tree species in the 26 forest stands is indi-

TABLE 1. Summary of Vegetation and Site Data: Plots A-1 to 7, Laniel; B-1 to 12, Black Sturgeon; C-1 to 6, Cedar Lake.

					BALSAM FIR			Basal area of other species as % of total stand										1950 Fb Seedlings 0" - 8'	1955 Fb Seedlings 0" - 8'
Plot	Site	Potential Plant Indicators	No. trees /acre	Total Basal Area Sq. Ft. /acre	% Fb of Total basal area	% Fb Dead (bas. area) 1950	% Fb Dead (bas.area) 1955	A	Bw	By	Mr	Ce	Pj	Pw	Sb	Sw	Misc.	No/acre ± 1·Se	No/acre ± 1·Se
A-1	2:1:4	a,b,f,h,v	1300	94	57	80	74	1	10	....	1	1	....	11	2	17	Tr.	9,880 ± 1040	7,150 ± 750
A-2	1:2:1	a,b,f,v	2300	139	63	87	58	....	17	2	....	....	....	9	....	4	5	2,020 ± 380	3,690 ± 690
A-3	1:1:2	b,d,p,q	1040	91	24	34	29	5	21	....	8	1	....	15	13	8	5	2,250 ± 480	2,630 ± 360
A-4	3:1:0	f,o,s,t	450	64	82	99	99	4	4	....	....	....	....	3	2	4	1	740 ± 110	320 ± 110
A-5	3:1:0	f,o,s,t	1080	101	68	99	99	10	1	....	....	....	....	4	8	6	3	480 ± 90	300 ± 110
A-6	3:2:0	f,o,s,t	590	93	86	99	100	3	2	....	....	....	....	4	1	3	1	1,180 ± 160	220 ± 130
A-7	2:2:3	b,f,t	1060	70	58	95	98	....	11	....	....	19	....	5	....	3	4	4,660 ± 690	2,800 ± 370
B-1	3:4:3	a,b	460	199	54	20	26	16	4	....	....	....	....	....	16	10	....	11,440 ± 1280	6,630 ± 670
B-2	2:2:3	a,b,e	400	132	65	13	94	8	7	....	....	....	....	....	4	16	....	9,370 ± 730	5,650 ± 500
B-3	3:2:4	a,b,e,k	1270	234	21	31	95	53	1	....	....	....	....	....	16	9	....	10,910 ± 630	7,370 ± 400
B-4	2:2:2	a,e,j,m	460	118	82	71	99	1	7	....	....	....	....	....	2	8	....	11,240 ± 790	6,160 ± 470
B-5 (A-H)	3:3:4	a,b,j,m	710	147	61	45	70	1	2	....	....	33	....	....	1	2	....	13,340 ± 980	6,210 ± 600
B-5 (I-T)	1:2:1	a,h,j	700	203	68	35	99	....	4	....	....	23	....	....	1	2	2	14,970 ± 970	8,960 ± 590
B-6	2:2:3	b,e,g,n,o	700	156	74	77	100	....	12	....	....	....	....	....	....	14	....	3,380 ± 480	2,820 ± 370
B-7	3:2:4	e,g,l,n	700	140	54	60	92	....	12	....	....	....	....	....	1	33	....	10,820 ± 660	7,200 ± 400
B-8	4:4:2	e,i,k,m	520	102	78	69	97	1	3	....	....	....	....	....	15	3	....	5,670 ± 510	3,790 ± 350
B-9	2:3:2	a,b,e	470	110	49	27	79	5	25	....	....	....	....	....	11	10	....	8,740 ± 610	7,520 ± 460
B-10	4:5:2	a,d,e,h,j,m	1560	267	63	69	92	....	2	....	....	33	....	....	1	1	....	13,770 ± 860	7,810 ± 470
B-11	2:2:2	a,b	1860	167	39	1	36	6	41	....	....	....	....	....	....	14	....	5,250 ± 850	3,680 ± 500
B-12	2:2:1	h,t	910	221	89	88	100	....	6	....	....	....	....	....	....	5	....	320 ± 170	280 ± 90
C-1	3:4:5	a,b,r,u	760	124	56	93	....	17	4	....	....	....	1	....	4	18	Tr.	3,220 ± 560	.....
C-2	2:2:6	b,e,u	530	141	21	73	94	4	20	....	....	....	38	....	8	9	Tr.	2,330 ± 780	2,220 ± 230
C-3	3:3:6	a,c,e	510	174	31	26	98	5	6	....	....	....	36	....	9	12	1	4,390 ± 540	2,700 ± 420
C-4	2:2:1	c,e,n,o,u	430	68	11	85	93	9	41	....	....	....	4	....	35	....	....	7,710 ± 520	5,260 ± 350
C-5	2:2:4	a,b,c,e	780	97	6	8	87	23	2	....	....	....	28	....	37	1	3	2,890 ± 280	2,300 ± 260
C-6	3:3:4	a,c,e,j,n,u	590	104	60	11	78	8	21	....	....	....	....	3	2	6	....	6,280 ± 2320	4,760 ± 680

TABLE 1—Continued.

Potential plant indicators listed by alphabetic symbols in Table 1.

Symbol Column 3	Scientific Name*	Symbol Column 3	Scientific Name*	Symbol Column 3	Scientific Name*
a	Aralia nudicaulis L.	g	Dalibarda repens L.	l	Linnaea borealis L.
b	Aster macrophyllus L.	h	Dicranum spp.	m	Lycopodium annotinum L.
c	Calliergon spp.	i	Equisetum sylvaticum L.	n	L. clavatum L.
d	Clintonia borealis (Ait.) Raf.	j	Hypnum spp.	o	L. obscurum L.
e	Cornus canadensis L.	k	Ledum groenlandicum L.	p	Maianthemum canadense Desf.
f	Corylus cornuta Marsh.			q	Mediola virginiana L.

*Nomenclature follows 8th Ed. of Gray's Manual of Botany, 1950

Colloquial names of trees listed by symbols above columns 9 to 17, Table 1.

A	trembling aspen	Mr	red maple	Pj	jack pine
Bw	white birch	Ce	white cedar	Pw	white pine
By	yellow birch				

Symbol Column 3	Scientific Name*
r	Poa spp.
s	Ribes spp.
t	Rubus idaeus L.
u	R. pubescens Raf.
v	Streptopus roseus Michx.

Symbol Column 3	Scientific Name*
Sb	black spruce
Sw	white spruce

cated by the data on the percentage of total basal area contributed by each species. For balsam fir, the percentage of total basal area dead at the time of the 1950 and the 1955 seedling tallies is also given. To some extent the picture given by the basal area data in Table 1 is a reconstruction, since mortality of budworm host trees was already advanced at the time some of the plots were established. A key to the colloquial names corresponding to the tree symbols used in the column headings is given at the foot of the table. Finally, the number of balsam fir seedlings per acre between ground level and 8 feet is given along with the standard error of the estimate.

Typical examples of the different soils found in the three study areas are given in Table 2. These descriptions include textural analysis of the soil, a description of the soil profile, the pH of each horizon, and a summary of the site characteristics. The four plots included in Table 2 are discussed separately in the following sections treating the vegetation and sites found in the three study areas.

Laniel, Quebec. This study area was centered around Laniel on Lake Kipawa, but included plots near the Little Jocko River, Ontario, 35 miles to the south, and one plot at Timagami, Ontario, 26 miles to the west. The Laniel district, 200 miles up the Ottawa River from the city of Ottawa, Ontario, lies on the northernmost fringe of Halliday's (1937) L4 Algonquin-Laurentides section of the Great Lake-St. Lawrence forest region. Halliday describes this area as follows:

> ". . . . the bedrock is part of the great Precambrian Shield of Canada, and consists largely of crystalline limestones, schists, and gneisses of the altered sedimentaries and granite intrusives. The topography is rough and irregular, and glacial deposits of varied character, chiefly of a light texture, cover the greater part. In addition there are some lacustrine deposits from the Nipissing-Great Lakes and Algonquin periods. . . .
>
> . . . . In this section, white pine (*Pinus strobus* L.) probably reached its maximum

TABLE 2. Soil Profile Descriptions of Representative Study Plots.

Horizon	Thickness	Color	pH	Percent by volume Sand	Silt	Clay	Col. Clay
		Plot A-1, Laniel; Ecoclimate 2; Moisture Regime 1; Pore Pattern 4.					
A_{00}	0-1″	brown	4.6				
A_0	1-2½″	black	4.6				
A_2	2½-6″	ashy gray	4.2	59	35	3	3
A_3	6-8″	gray-brown	4.8	57	38	2	3
B_2	8-14″	chocolate brown	5.0	62	33	2	3
B_3	14-18″	brown-gray	5.0	87	11	1	1
C_1	18-25″	gray	5.9	82	15	1	2
D	Bedrock						
		Plot A-5, Laniel; Ecoclimate 3; Moisture Regime 1; Pore Pattern 0.					
A_{00}	0-1″	dark brown	4.4				
A_0	1-3″	dark brown	4.3				
A_2	3-5″	ashy gray	4.0	74	22	2	2
B_2	5-9″	chocolate brown	4.4	86	13	0	1
B_3	9-15″	light brown-yellow	4.9	74	23	2	1
C	15-30″	yellow gray	4.3	93	6	1	0
D_1	30-35″	gray	4.3	94	5	1	0
		Plot B-5 (A-H), Black Sturgeon; Ecoclimate 3; Moisture Regime 3; Pore Pattern 4.					
A_{00}	0-1½″	dark brown	5.6				
A_0	1½-2½″	dark brown	5.9				
A_1	2½-3″	medium brown	5.9				
A_2	3-3½″	medium gray	5.7	67	28	2	3
B_1	3½-6″	light brown	5.6	82	14	trace	4
B_2	6-12″	chocolate brown	5.7	87	10	0	4
B_3	12-19″	yellow brown	5.9	94	4	trace	2
C	19-25″	yellow brown	6.7	96	3	trace	1
C	25-40″	yellow brown	6.8	97	1	1	1
D_1	40-50″	medium gray	6.3	25	38	13	24
D_1	50-72″	light gray	8.3	15	37	16	32
D_2	72-	gray	8.2	94	4	1	1
		Plot C-3, Cedar Lake; Ecoclimate 3; Moisture Regime 3; Pore Pattern 6.					
O_{00}	0-1½″	light brown					
A_0	1½-3½″	chocolate brown	4.3				
A_1	3½-4″	black					
A_2	4-9″	gray	5.1	20	23	4	53
B_2	9-21″	medium brown	6.1	13	22	6	59
B_2	21-33″	medium brown	6.7	17	16	4	62
B_3	33-46″	gray-brown	7.7	15	26	10	47
C	46-63″	brown-gray	8.6	16	38	16	30
G	63-76″	mottled gray	8.8	16	55	6	23

development in Canada. . . . Red pine (*Pinus resinosa* Ait.) has also been a prominent species. . . . In spite of the previous dominance of these species and the presence of intrusive conifers from the Boreal Forest Regions, the general character is that of a mixed forest and the dominant . . . association is one of sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula lutea* Michx. f.), hemlock (*Tsuga canadensis* (L.) Carr.), and white pine. In addition there are varying amounts of basswood (*Tilia americana* L.), white spruce, balsam fir, beech (*Fagus grandifolia* Ehrh.) (Northern) red oak (*Quercus rubra* L. var. *borealis* (Michx.f.), elm (*Ulmus americana* L.), white ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.), ironwood (*Carpius caroliniana* Walt.),

white birch (*Betula papyrifera* Marsh.), and large-toothed aspen (*Populus grandidentata* Michx.)."

Two different types of site were studied in the Laniel region. Plots A-1, A-2, A-3, and A-7 were located on loamy sandy till, and plots A-4, A-5, and A-6 on outwash sand. In Table 2, the soil profile of plot A-1 is described as an example of the till plots, and that of plot A-5 as an example of the plots on outwash sand. The soil of plot A-1 was derived from a stony sandy till that covered granitic bedrock to a depth ranging from 6 inches to 3 feet. Over 50 percent of the volume of the mineral soil was found to be made up of particles greater than one-tenth of an inch in diameter. Although the coarse sand constituents facilitated rapid internal drainage, the silt content retained sufficient available water for plant growth. Moreover, the proximity of the bedrock to the surface prevented the gravitational water from draining away too rapidly.

The soil on plot A-5 has a very high proportion of coarse sand except for a few areas with silt, probably of loess origin, in the A_2 layer. Excessive drainage, indicated by a moisture regime of index 1 and a pore pattern of index 0, has facilitated the formation of an extremely well-developed A_2 horizon and a comparatively shallow B horizon. In this plot the excessive aridity of the upper horizons was conducive to the rapid establishment and dense growth of raspberry (*Rubus idaeus* L.) following tree mortality after the budworm infestation. This plant now constitutes the chief competitor to tree seedlings.

Balsam fir in the Laniel region is not very abundant, but it occurs in pockets where the water supply is adequate. From 24 to 86 percent of the basal area of the Laniel plots was balsam fir, with the higher percentages occurring on the water-washed sand sites. On these sand sites balsam fir suffered uniformly high mortality due to budworm defoliation. The greatest productivity in terms of total basal area and total stem numbers was recorded on plot A-2, where the soil was composed of a sandy loam with adequate moisture and a warm ecoclimate. "Productivity" in these terms is not necessarily synonymous with its meaning in forest industry, for it is noteworthy that the average diameter of trees on plot A-2, which may be calculated from the data in columns 4 and 5 of Table 1, was only 3.3 inches, while the average diameter of trees on plot A-4, lowest of the Laniel plots in stem numbers and basal area, was 5.1 inches. Having regard for possible differences in stand development and the observed differences in species composition, however, it is probably safe to conclude that the outwash sands have a lower productive capacity than the loamy tills. White birch and white pine, for example, while present on all plots, were both notably more abundant on the till plots, A-1, A-2, A-3, and A-7. White cedar, *Thuja occidentalis* L., was of consequence only on plot A-7 where the soil was less acid and contained almost 50 percent silt by volume, the highest proportion of silt measured on the Laniel plots.

Balsam fir seedlings were found to be substantially more abundant on the till plots than they were on the coarse sands at the time of the 1950 tally, a differential that was maintained in the reduced numbers of seedlings found during the 1955 tally. The most striking characteristic in the soil profiles on the water-washed sands is the well-developed sterile A_2 horizon, and it is therefore tempting to generalize that such sterile surface horizons must have a detrimental influence upon the abundance of balsam fir seedlings. In the previous paragraph we noted, however, that in the original stands which supported the budworm outbreak, balsam fir contributed the greatest proportion to the basal area of stands on the sand sites. This, then, presents an anomalous situation, since these original satnds became established on what must have been essentially the same soil profiles. The answer to the problem may lie in the early history of the budworm out-

break at Laniel. Another field party, working in the same stands where the sand plots were later established, found that the mortality of overstory balsam fir was already well advanced as early as 1947, and that the ground had become dominated by an almost impenetrable growth of raspberry at that time (H. M. Thomson, personal communication). It seems likely, therefore, that the 1950 tally of the sand plots is an inadequate representation of the seedling population before budworm disturbance, and that it would be unwise to generalize correlations between seedling abundance and site conditions from these data.

Black Sturgeon Lake, Ontario. This study area was centered around the 12-mile length of Black Sturgeon Lake, 70 miles northeast of Port Arthur, Ontario. One plot, B-11, was established on the Sibley Park peninsula 20 miles east of Port Arthur. This district lies in Halliday's (1937) B.9 Superior Section of the Boreal Forest Region. Halliday describes this section as follows:

> ". . . . Terraces and other lacustrine deposits from glacial Lake Algonquin and its predecessors are common in these valleys and on the southward-facing slopes, bordering the lake. Glacial deposits cover most of the ground, but much exposed rock is present—a condition greatly strengthened by the severe burning to which this section has been subjected.
>
> The geologic structure consists of Precambrian granites with areas of late Precambrian iron slates, sandstones, and conglomerates, with block-faulting and diabase intrusion.
>
> The presence of white spruce associations with some balsam fir, balsam poplar (*Populus balsamifera* L.), and white birch, especially on the river terraces, is possibly a characteristic feature of the section. . . . On slopes and lower hill-tops, where heavier glacial deposits can be found, mixed associations of black spruce, white birch, white spruce, and some aspen and balsam fir are common. . . . Lower and poorly drained positions support black spruce and tamarack (*Larix laricina* (Du Roi) K. Koch) with a scattering of Eastern white cedar. . . ."

Soil investigations in the Black Sturgeon Lake district indicate that a large, short-lived glacial lake occupied this valley, and that its waters extended several miles westward. Substantiating evidence includes a widespread uniform stratum of silt loam about 3 feet in thickness lying under several feet of water-washed sand. This layer of silt loam serves as a source of nutrients, and is sufficiently close to the surface to prevent a too-rapid drainage of gravitational water from the overlying sand. Plots B-1, B-3, B-5 (A-H), B-5 (I-T), and B-10 are located on this type of site.

This sand-over-silt arrangement is evident in the soil profile of plot B-5 (A-H), given in the third section of Table 2, in which the demarcation between the two depositions is obvious at the 40-inch level. The high silt loam and clay content of the deeper layer is shown in the textural analysis of the D_1 horizon (40 to 72 inches). The D_1 layer is underlain by a sandy D_2 stratum. Most of the tree roots were within the upper 18 inches, although some extended to a depth of 3 feet. This type of site appears to be the most consistently productive of those measured in the Black Sturgeon area. The superiority of this site can be demonstrated in a simple test of rank correlation. If the basal area figures for the 13 plots be assigned ranks from 1 to 13, plots B-10, B-3, B-5 (I-T), B-1, and B-5 (A-H) attain the ranks 1, 2, 4, 5, and 8 respectively, giving a rank total of 20. Of the 1,287 unique combinations of 5 ranks which may be taken from a total of 13, only 18 give a total as low or lower than 20. The superiority of this site therefore achieves a significance of 18/1287, which lies between the one and two percent levels. The basal area of trees on the five plots on this type of site averaged 210 square feet per acre, while the basal area of trees on the eight plots on other sites in the area averaged only 143 square feet per acre. Free calcium from the silt layer produced a high pH on plots B-5 (A-H, B-5 (I-T), and B-10, and thus favoured

the establishment of alkaliphilous white cedar.

The forest stands studied in the Black Sturgeon Lake area represent various stages of boreal forest succession tending towards a more or less stable climax association of balsam fir and white spruce. Plot B-3 represents a typical pioneer stage, with shade-intolerant aspen constituting 53 percent of the total basal area, while the tolerant species, balsam fir, white spruce, and black spruce, together comprised only 43 percent of the basal area. Plots B-9 and B-11 have a comparable proportion of intolerant hardwoods, although the lighter, sandy soils on these plots have favoured the predominance of white birch. Aspen occurs characteristically as a pioneer species on the heavier soils in this area, such as those of plots B-1 and B-3.

Of the Black Sturgeon Lake plots, only plot B-12 is notable for its low numbers of balsam fir seedlings. This plot was situated at a point very close to the center of the Lake Nipigon budworm infestation, on an outwash sand similar in profile development to plots A-4, A-5 and A-6 at Laniel. Plot B-12 has also been heavily overgrown with raspberry since the time of its establishment in 1949, so that, with a similar history of advanced overstory mortality before the first regeneration tallies on the plot, it is again questionable if relations between profile development and seedling abundance can be inferred without reservation. In this connection it is noteworthy that plot B-12 ranked third among the Black Sturgeon plots in productivity as measured by total basal area before budworm disturbance. Since 89 percent of the original 221 square feet of basal area was balsam fir, it is apparent that the stand destroyed by the spruce budworm on this site originated from a substantial crop of balsam fir seedlings that established themselves on essentially the same profile at that earlier time.

Cedar Lake, Ontario. This study area was centered around the Cedar Lake-Lac Seul district which lies 90 miles to the northeast of Kenora in northwestern Ontario. This district lies in Halliday's (1937) B.11 Western Transition Section of the Boreal Forest Region, with more typical boreal forest to the north, and with the Great Lakes-St. Lawrence forest to the south. Halliday describes this section as follows:

> " . . . . The main body of the forest cover . . . consists of associations of jack pine (*Pinus Banksiana* Lamb.) with black spruce and mixtures of white and black spruce, white birch, aspen and some balsam fir, where the deeper soil deposits are found. Swampy depressions contain black spruce, but tamarack is not very abundant. . . .
>
> The section . . . . has a rough and rolling topography with very numerous lakes. Having been strongly glaciated and also not influenced by glacial Lake Agassiz, the soils are generally thin, with occasional moranic ridges and much exposure of the underlying rocks of the Precambrian Shield."

Five of the six plots in the Cedar Lake district were located on heavy soils. The one exception, plot C-4, was established on a sandy till comparable to similar sites at Laniel and at Black Sturgeon Lake. The soil profile of the plot C-3, typical of the heavier soils at Cedar Lake, is given in the fourth section of Table 2. The silt content of these heavier soils tends to increase with increasing depth, so that good regional drainage is facilitated. The varved clays of this area are usually underlain by a sandy till at the eight-foot depth. The soil is alkaline in its reaction, and the presence of free carbonates at a depth of about 40 inches was detected by the dilute hydrochloric acid test. The water table is usually about 5 feet below the surface. Root penetration is largely limited to the upper 18 inches, although the occasional deep root may extend to a depth of 3 feet.

The sandy soil of plot C-4 had the lowest productivity in terms of total basal area of the sites sampled in the Cedar Lake area. This site was also notable, however, for having the largest number of balsam seedlings per acre, so that the productivity of this site may appear to be substantially better when the next stand is

mature. Plot C-3, on a 3:3:6 site, with a total basal area of 174 square feet per acre, was the most productive of the six plots. Forest stands in the Cedar Lake area had a much greater proportion of jack pine, and an appreciably lower content of balsam fir, than stands on similar sites at Black Sturgeon Lake or at Laniel. This is probably a result of the more arid climate which Chapman (1953) has shown to prevail in this part of northern Ontario. It may be that balsam fir becomes of greater consequence in this area as the pioneer jack pine deteriorates in stands undisturbed by fire, logging, or insect damage.

Mortality in Relation to the Percentage of Balsam Fir

Inspection of columns six, seven, and eight of Table 1 will reveal that, in general, the mortality of balsam fir tends to be high when the percentage of total basal area contributed by balsam fir is high, and to be lower when this percentage is low. This relationship has been analyzed and discussed at length by Turner (1952) for data collected in the Algoma forest area of Ontario. Turner concluded that balsam fir mortality was related to the percentage of balsam fir in the stand, and to the actual basal area of balsam considered independently of other species. Data collected in the present study afford an opportunity to assess the generality of Turner's conclusions.

Recent developments in the field of non-parametric correlation statistics provide methods of analysis better suited to the treatment of percentage data than the conventional normal curve statistics. Non-parametric correlation methods are especially to be preferred with data as grossly skewed as the percentage mortality data in this study. Kendall's (1955) "tau" statistic provides a method of rank correlation involving no assumptions as to the form of the distribution, and is therefore well suited to the analysis of these data. The "tau" statistic is a correlation coefficient similar to the familiar "rho" or $r_{x.y}$ coefficient, and has the same range from $+1$ to -1. In general, the calculation of "tau" yields a more conservative value for the same data than the calculation of "rho." "Tau" has been used to some extent in psychological research, in which field the desirability of non-parametric statistics arises from problems of distribution similar to those encountered in field ecology.

Results obtained with this statistic are presented in Table 3. Ranks assigned to the percentage of total basal area data have been arranged in the natural order 1, 2, 3, . . . , throughout the six tests, and below these the ranks assigned to the mortality data from the corresponding study plots fall as they will. Thus the Laniel plots appear in the order A-3, A-1, A-7, A-2, A-5, A-4, and A-6, a ranking order from the lowest to the highest percentage of balsam fir that may be readily confirmed from inspection of column six, Table 1. In Table 3, ties in rank are indicated either by the repetition of a digit when an odd number of ranks are tied, or by the use of the fraction one-half when an even number of ranks are tied.

All six tests yield a positive value for the correlation coefficient, and for the Laniel and Black Surgeon Lake data these values are substantial and strongly significant. Probability values were calculated by means of the normal approximation, the assumption of normality being made for the distribution of the test statistic, and not for the original data. Although the correlation coefficients for the Black Sturgeon Lake data are smaller than those for Laniel, the greater number of plots upon which the Black Sturgeon Lake values are based give to these values an appreciably greater significance. The 1950 data for Cedar Lake would be compatible with a hypothesis of independence of the two variables. Agreement between the rankings in 1955 is more satisfactory however, four of the five plots falling in exactly the correct order. The low number of plots at Cedar Lake makes any analysis of these data un-

TABLE 3. Kendall's "tau" statistic as a measure of the correlation between ranked values of balsam fir mortality and the percent of total basal area contributed by balsam fir.

Study Area	Year		Ranks													"tau"	p[1]
Laniel	1950	% Fb	1	2	3	4	5	6	7							+.750	.03
		% Mort.	1	2	4	3	6	6	6								
	1955	% Fb	1	2	3	4	5	6	7							+.759	.02
		% Mort.	1	3	4	2	5½	5½	7								
Black Sturgeon Lake	1950	% Fb	1	2	3	4½	4½	6	7	8	9	10	11	12	13	+.585	.004
		% Mort.	5	1	4	3	8	7	9½	2	6	12	9½	11	13		
	1955	% Fb	1	2	3	4½	4½	6	7	8	9	10	11	12	13	+.579	.006
		% Mort.	8	2	4	5½	1	3	5½	7	10½	12½	9	10½	12½		
Cedar Lake	1950	% Fb	1	2	3	4	5	6								+.067	.42
		% Mort.	1	5	4	3	6	2									
	1955	% Fb	1	2	3	4	5									+.200	.41
		% Mort.	2	3	4	5	1										

[1]Probability values for the significance of "tau" calculated by means of the normal approximation.

reliable, and these figures are offered only for comparison.

Turner's (1952) conclusion that mortality increases with increasing percentage of balsam fir is substantiated by the Laniel and Black Sturgeon Lake data. It is perhaps to be expected that mortality should be strongly correlated with the percentage of total basal area contributed by balsam fir, for if, as Blais (1952) and Bess (1946) have shown, an exposed, flowering balsam fir tree is more liable to severe defoliation, it follows that in a stand where nearly the entire basal area is contributed by balsam fir, most balsam trees will of necessity be exposed, and defoliation and mortality will be severe. Conversely, in a stand where only a small proportion of the total basal area is contributed by balsam, these trees will in all likelihood be surrounded and perhaps overtopped by trees not susceptible to budworm attack.

Turner found that he was able to conduct a satisfactory analysis using the actual basal area of balsam fir, considered independently of its relation to the basal area of other species in the stand. Attempts to correlate the actual basal area of balsam fir and percent mortality with the "tau" statistic failed to produce significant correlation coefficients, although again all six coefficients were positive, a uniformity that suggests a real bias in this direction.

Relative Abundance of Shrub Species

During the 1955 re-tally of the study plots, an attempt was made to record all shrub species present on each milacre quadrat which had grown, or which were capable of growing, to a height or density sufficient to compete with tree seedlings. No annuals present on the plots satisfied these restrictions, but small perennials such as *Vaccinium*, *Diervilla*, and *Lonicera*, which grow in persistent clumps, were included. White birch seedlings and trembling aspen sucker growth were also included if they were sufficiently advanced to merge with the general level of the shrub layer.

During subsequent analysis, the number of quadrats on which each species of shrub had occurred was determined, and the various species were then arranged in rank from the most to the least abundant. When these data were plotted in bar-graph form, the relationship illustrated in Figure 2 became apparent. In the graphs for all 25 study plots for which these data were available, the relation between successively less abundant species was distinctly curvilinear.

Data for two plots from each of the

three study areas are illustrated in Figure 2. The uppermost number on each of the ordinate scales is given as a fraction, the denominator of which indicates the total number of milacre quadrats on the entire plot. The numerators of these fractions are continuous in series with the remainder of the ordinate scales, which may be considered as sharing the denominator given in the uppermost fraction. The ordinate scale thereby provides an index of the relative abundance of the various shrubs. The abscissa scale indicates the rank in order of abundance of each successive species. This rank is given alphabetically, and ties in rank are indicated by a repetition of the appropriate letter.

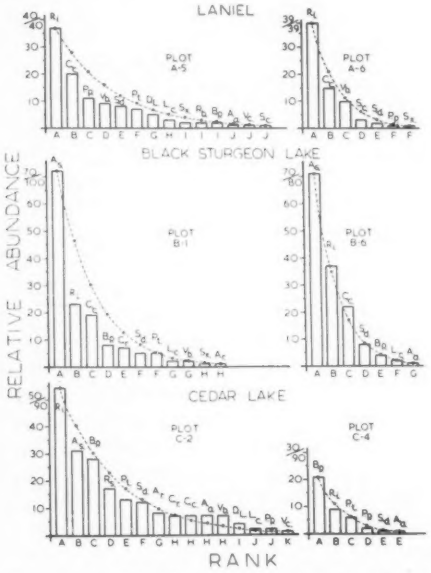

FIGURE 2. *Curvilinear progression in relative abundance of shrub species arranged in the order of their frequency of occurrence. A.a.:* Amelanchier alnifolia *Nutt.*; *A.r.:* Alnus rugosa *(Du Roi) Spreng.*; *A.s.:* Acer spicatum *Lam.*; *B.p.:* Betula papyrifera *Marsh.*; *C.c.:* Corylus cornuta *Marsh.*; *C.r.:* Cornus rugosa *Lam.*; *D.L.:* Diervilla Lonicera *Mill.*; *L.c.:* Lonicera canadensis *Bartr.*; *P.p.:* Prunus pensylvanica *L.*; *P.t.:* Populus tremuloides *Michx.*; *Rb.:* Ribes *sp.*; *R.i.:* Rubus idaeus *L.*; *Rs.:* Rosa *sp.*; *S.c.:* Sambucus canadensis *L.*; *S.d.: Sorbus* (=Pyrus) decora *(Sarg.)*; *Sx.:* Salix *sp.*; *Vb.:* Viburnum *sp.*; *Vc.:* Vaccinium *sp.*

Also given in these graphs, for comparison with the observed series, is the exponential series that may be fitted between the most and the least abundant species in the number of steps indicated by the number of shrub species present on the plot. This series has been used to illustrate the curvilinear nature of the data, but it would be premature to infer from the very satisfactory agreement in several of the illustrated instances that the relationship was exponential. The observation of a few species at a high level of abundance, and a relatively substantial number of species at a low level of abundance, suggests that the hyperbola may provide an equally satisfactory description of the relationship. The more important point brought out by the present data is that this relationship is clearly non-linear. The significance of this non-linearity as evidence of interspecific competition is apparent if one considers that by plotting unrelated frequencies in order of rank, as, for example, a series of "frequencies" drawn from a table of random numbers, the scatter of points so obtained falls about a straight line, the slope of which is inversely proportional to the number of draws.

It must be pointed out that these data were collected without any particular analytical approach in mind, so that there was no opportunity to guard against specific errors which might bias the shape of these curves. At the same time, there is no possible source of error in this work sufficiently great to have brought about the distinctly non-linear nature of these data throughout all 25 study plots. It is therefore concluded that the frequencies of occurrence of successively less abundant shrub competitors are related in some curvilinear manner.

Competitive Abilities of Balsam Fir and Spruce Seedlings

The quotations from Craighead (1924) and de Gryse (1944) given in the intro-

duction indicate that there has been some difference of opinion as to the relative competitive abilities of balsam fir and spruce seedlings. Ideally, we should bring to this problem a detailed knowledge of the flowering histories of overstory balsam fir and spruce trees in the stands under investigation, along with experimental data on the germination of their respective seeds on various sorts of ground litter, the subsequent survival of these seedlings during the first two or three years of growth, and data on the growth rate of established seedlings both under suppression and following release by removal of the overstory. While techniques for measuring the flowering histories of balsam fir trees have been investigated in relation to other problems under study at this laboratory, these techniques are still too unwieldy for all but a few special studies of which they form an essential part. Similarly, direct experimentation with the germinative ability of balsam fir and spruce seeds lies outside the scope of this investigation.

Fortunately, these deficiencies in our knowledge bear upon an aspect of the problem which may be separated from the main questions raised by Craighead and de Gryse. Questions of seed supply, germinative ability, and survival during the earlier years of growth, are clearly of consequence in relation to the relative numbers of established seedlings of the two species. Once given established seedlings, however, we are then concerned only with the relative growth rate of the two species under suppression and following release, and the data from the 1950 and 1955 seedling tallies are directly applicable to the problem. It seems advisable, at this point, to anticipate a part of the results that will appear in the second paper in this series, and to state that in the areas studied, the overwhelming majority of balsam and spruce seedlings that are forming the new stands following budworm devastation were already established before the budworm outbreaks. For this reason we may set to one side the question that de Gryse raised in connection with the relative rooting ability of the two species on the "extraordinary accumulation of debris on the surface" following overstory mortality.

Data from the two seedling tallies allow us to compare the distributions of seedlings by species and height class as these were found in 1950, when release through overstory mortality had not appreciably influenced these distributions, and again in 1955, after the seedlings had benefitted from at least five years of rapid growth. In Figure 3 the distributions by height class are given for balsam fir and spruce seedlings on plot B-8 at Black Sturgeon Lake, and on plot C-4 at Cedar Lake. The upper pair of histograms represent the 1950 tally, and the lower pair the 1955 re-tally. Since balsam fir seedlings outnumbered spruce seedlings in all height classes in both tallies on these plots, comparison of the distributions has been facilitated by superimposing the distributions of spruce seedlings, in black, on the distributions of balsam fir seedlings. Beside each histogram the estimate of total seedlings per acre is given, and the average height of seedlings is entered at the appropriate point above the distributions. "Spruce" in this, as in other parts of this paper, refers to both black and white spruce. Black spruce constituted only ten percent of all spruce seedlings tallied on the plots, and did not provide satisfactory data for separate analysis.

The data for plot C-4 illustrate the remarkable similarity found between distributions of balsam fir and spruce seedlings, when substantial numbers of spruce were available for comparison with the universally abundant balsam fir. It is apparent that the spruce distribution in 1950 was simply a replica on a smaller scale of the balsam fir distribution, and that both distributions shifted together into the upper height classes during the following five years. The same pattern is evident, though less well marked in the data for plot B-8. Minor discrepancies in the heights of comparable histogram bars illustrated in this instance are characteristic of these distribu-

tions for the many plots on which there occurred only a few hundred spruce seedlings per acre. Even in the absence of more elaborate data from other studies, the 1955 graphs for both plots would strongly suggest that there had been no recruitment of new seedlings in the lower height classes following overstory devastation.

The overall similarity between distributions of spruce and balsam fir in both tallies suggested that no serious bias would result if each distribution was represented by its mean so that the paired "t" test could be used to assess the minor differences between average heights of balsam fir and spruce seedlings. This test indicated that these differences did not significantly favor spruce or balsam fir in either tally, and that there is, therefore, no evidence in these data of a consistent difference in the growth rates of these species under suppression or immediately following release. The possibility remains that future re-tallies of these plots may disclose such differences during later stages in the development of the new forest stands. The important point that may be taken from the present study, however, is that any minute differences that may exist, being at best too small to be reflected in the distributions by six-inch or one-foot height classes, are unlikely to be of any consequence in interspecific competition at the seedling level. That there should be no such gross differences seems in keeping with the picture of two such ecologically similar species found commonly in competitive association.

Decrease in Seedling Numbers Between the 1950 and 1955 Tallies

When the 1955 regeneration tallies were analyzed, it became apparent that there had been a decrease of from 20 to 65 percent in numbers of balsam fir and spruce seedlings since the previous tally of these plots in 1950. Examination of the seedlings per acre figures in Table 4, particularly data for balsam fir seedlings on the Black Sturgeon Lake plots, will disclose that during the five-year interval between tallies there was a decrease of five to six thousand seedlings per acre on some plots. To some extent this decrease had been anticipated, and provision was made on the 1955 tally sheets to record certain relevant data. These data included the number of dead seedlings on the quadrats, the extent to which the quadrats were covered by windbroken, budworm-killed trees, and the extent to which shrub growth appeared to be choking out established seedlings.

The tally of dead seedlings accounted for very little of the reduction in seedling numbers. Only 1.4 percent of the decrease in spruce seedlings and 0.9 percent of the decrease in balsam fir seedlings could be accounted for in this way. The attempt to correlate the decrease in seedling numbers with coverage of the quadrats by broken trees proved considerably more rewarding, however. Coverage by broken trees was estimated in fifths, i.e.: 0/5, 1/5, . . . , 5/5, corresponding to a series of 20 percent classes. These simple fractions seem to lend themselves to estimation in the field with less subjective error than percentages, and the similarity in the overall estimates of

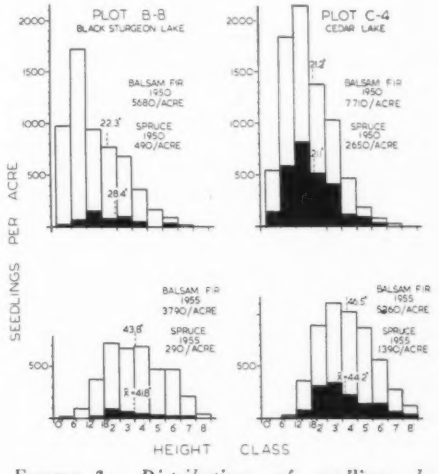

FIGURE 3. *Distributions of seedlings by height classes for representative plots from Black Sturgeon Lake and Cedar Lake. Spruce distributions superimposed in black on the distributions for balsam fir.*

different workers tallying separate sections of the same plot was encouraging. For analysis, the estimate for each quadrat was converted to a decimal fraction, and the total for all quadrats averaged to give a single estimate of coverage by broken trees for the plot.

The correlation between per cent coverage by wind-broken, budworm-killed trees, and the percent decrease in numbers of balsam fir seedlings between the two tallies, is illustrated in Figure 4. Spruce data were not used in this analysis, since the estimates of spruce seedlings per acre are based on small numbers and are consequently less reliable than the estimates for balsam fir. Some of the broken trees noted at the time of the 1955 tally were undoubtedly on the ground in 1950, but the great majority may safely be assumed to have fallen between 1950 and 1955. Data from plots A-2 and A-3 were irrelevant to this study, and were edited; on these plots, many of the overstory balsam fir survived the budworm outbreak and provided a seed source for the establishment of new seedlings during the period between tallies. Data available for this analysis were further reduced by the destruction of plot C-1 at Cedar Lake by road construction.

A correlation coefficient of $+0.846$ was found to express the strength of the relation between these variables; with the 21 degrees of freedom available in this analysis the coefficient is significant beyond the 0.001 level. From the square of the correlation coefficient it appears that approximately 72 percent of the decrease in numbers of balsam fir seedlings can be attributed to coverage by fallen trees.

Shrub growth on the quadrats was rated as *none*, *trace*, *competing*, *retarding*, or *choking*, in relation to its apparent effect on the growth and survival of balsam fir and spruce regeneration. Again the similarity of estimates by different workers was encouraging in view of the highly subjective nature of the rating system. Ratings of *competing* or below were assigned to shrub growth that appeared too scant to influence survival of the seedlings. Ratings of *retarding* or *choking* were assigned to shrub growth which nearly or completely pre-empted the quadrat. On many of the quadrats on which the shrub growth was rated as *choking*, a thorough check for the presence of dead seedlings under fallen trees and within the dense shrub growth could not have been conducted without destroying the conditions as they existed on the quadrat.

The percent of quadrats to which the ratings *retarding* or *choking* had been assigned was calculated for each plot. Analysis of these estimates for correlation with the decrease in seedling numbers yielded a value of $+0.403$ for the conventional $r_{x.y}$ coefficient, and a value of $+0.275$ for Kendall's "tau" coefficient. With the 21 degrees of freedom available in these analyses, both coefficients attained a one-the two-tailed test fell just short of the 5 percent significance level in each instance, there is adequate *a priori* justification for interest in only the single-tailed test in this analysis. Squaring the $r_{x.y}$ coefficient indi-

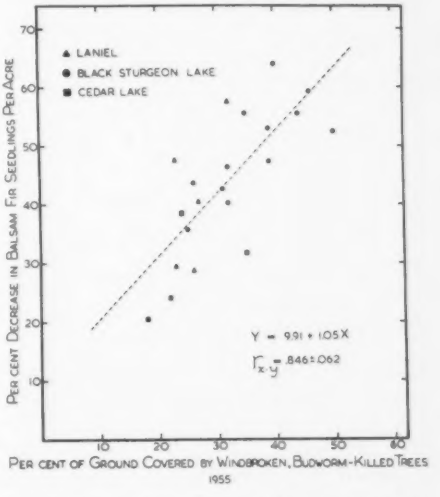
▲ LANIEL
● BLACK STURGEON LAKE
■ CEDAR LAKE
Y = 9.91 + 1.05X
$r_{x.y}$ = .846±.062
PER CENT DECREASE IN BALSAM FIR SEEDLINGS PER ACRE
PER CENT OF GROUND COVERED BY WINDBROKEN, BUDWORM-KILLED TREES 1955

FIGURE 4. *Correlation and regression of the decrease in balsam fir seedling numbers against coverage of the ground by wind-broken, budworm-killed trees.*

cates that approximately 16 percent of the decrease in seedling numbers can be attributed to shrub competition.

Field experience during this study left the impression that coverage by broken trees and density of shrub growth were simultaneous expressions of a third factor, the extent to which the various stands had been opened by budworm devastation. Analysis for correlation between the estimates of shrub density and the estimates of coverage by broken trees yielded an $r_{x.y}$ coefficient of $+0.502$, significant at the 1 percent level. In an earlier section we have already confirmed Turner's (1952) conclusion that the opening up of these stands, as measured by the mortality of balsam fir, bears a strong correlation to the percentage of total basal area contributed by balsam fir. In short, we are faced with a web of interrelated causes and effects in which one cannot be certain that statistically related variables bear causal relations to each other. For this reason, it is probable that the 16 percent of the decrease in seedling numbers attributed to shrub competition is not totally independent of the 72 percent of this decrease attributed to coverage by broken trees. However, we can say with confidence that, taking together the tally of dead seedlings and the correlations of shrub competition and coverage by broken trees with the decrease in seedling numbers, we can account for between 75 and 90 percent of the seedling mortality. We are left, therefore, at worst with only 25 percent of total mortality to attribute to unmeasured factors and to observer error in the two tallies.

Trends in Forest Succession

The present study has been guided by the possibility that spruce budworm devastation may effect a preponderance of balsam fir over spruce in the succeeding stand, or, in a parallel situation, that this devastation may effect an increase in such preponderance of fir as may already exist. At present it is possible to make three relevant comparisons within the data gathered during this study: the 1950 regeneration tally may be compared to the original tree tally for evidence of disproportionate reproduction by the seed trees; the 1955 regeneration re-tally may be compared to the 1950 regeneration tally for evidence of possible differences in survival and in the establishment of new seedlings; and finally, the 1955 re-tally may be compared to the tally of the original stands for evidence of a return to, or a further departure from, the balsam fir-spruce ratios as these originally existed.

A comparison of the 1950 regeneration tally with the original tree tally. Data on the basal areas of spruce and balsam fir in the original stands, while available for future use, will be of little value until the new stands approach a stage of development comparable to that at which the previous stands were destroyed. At present the most meaningful data from the original stands are the data on stems per acre. Their use tends to indicate a greater preponderance of balsam fir than would be suggested by basal area or volume data, since the diameters of spruce encountered on the study plots were at least equal to, and often substantially greater than those of the balsam fir.

Data on stems per acre of balsam fir and spruce are given in columns two and three of Table 4. The quotient obtained by dividing the number of fir stems by the number of spruce stems is given in ratio to unity in column four. It is clear that fir stems greatly outnumbered spruce stems in the original stands, a situation that was reversed on only 2 of the 26 study plots, plots B-3 and C-4. Estimates of seedlings per acre obtained from the 1950 regeneration tally are given in columns five, six, and seven. Again the balsam fir greatly outnumbered the spruce, approaching equality only on plot A-5. Taking as an example plot A-1, the ratio of 15 balsam fir stems to every spruce stem in the original stand increased to a ratio of 31:1 in the 1950 regeneration tally, so that the apparent trend is noted as

increasing in column eight. Similar comparisons will confirm that the remaining Laniel plots, A-2 to A-7, all show a decrease on this basis, while all Black Sturgeon Lake plots, B-1 to B-12, show a moderate to substantial increase. Two of the Cedar Lake plots show a decrease, and the remaining four, a slight to moderate increase.

In the lower left-hand corner of Table 4 these trends have been analyzed for regional independence in a 2 x 3 contingency table. Expected values under the hypothesis of regional independence are bracketed beneath the observed frequencies. Without reference to the large chi-square, it is apparent that the trend in forest succession which one may measure by these methods is strongly dependent upon the particular area in which the observations are made. One cannot argue, for example, that the overall ratio of 18:8 between *increasing* and *decreasing* trends demonstrates that balsam fir reproduces itself disproportionately to spruce, for this ratio depends for its value directly upon the number of plots located in the three study areas, and might have been reversed if more plots had been established at Laniel, and less at Black Sturgeon Lake. It is therefore concluded that, given the right circumstances, both balsam fir and spruce are capable of disproportionate reproduction, and that our knowledge of the circumstances that may favor the one or the other is as yet too meagre to permit prediction of the pattern of forest succession following a given outbreak of the spruce budworm.

A comparison of the 1955 and 1950 regeneration tallies. Comparable data on seedlings per acre and the ratios of balsam fir to spruce seedlings for the 1955 tally are presented in columns nine, ten, and eleven of Table 4. Taking, for example, the ratio of 38:1 observed on plot A-1, and comparing this to the ratio of 31:1 observed in 1950, there was an apparent increase in the ratio of fir to spruce seedlings during the five-year interval between tallies. There was a similar increase on all seven of the Laniel plots during this period, while eight of the Black Sturgeon Lake plots showed a decrease. No measurable change took place during this interval on two of the Black Sturgeon Lake plots, B-2 and B-12, while on the remaining three plots, B-6, B-8 and B-10, there was a slight increase in the preponderance of balsam fir. All but one of the five plots still available for measurement at Cedar Lake in 1955 showed a decrease in the ratio of balsam fir to spruce.

These trends are analyzed for regional independence in the lower right-hand corner of Table 4. Again a comparison of the expected and observed frequencies suffices to indicate that the trend in forest succession measured by these methods is strongly dependent upon the region in which it is made. Most of the changes in ratio between tallies are minor, and may be attributed to the vagaries of "sampling" by falling trees, particularly when the seedlings tend to grow in clumps that may be spared or wiped out as a unit. It has been shown in an earlier section that over 70 percent of the decrease in balsam fir seedlings can be attributed to coverage by broken trees. With so small a remainder it is pointless to attempt to show a difference between spruce and balsam fir seedlings in their inherent tenacity under competition. However, several features of the data presented in this study suggest that the difference is either minute or non-existent. The overall ratio of 11:12 between *increasing* and *decreasing* trends in this latter contingency analysis lends no support to the hypothesis that there is an inherent difference in survival independent of the region in which it is observed. Moreover, one would expect a real difference in survival rate to be reflected in consistently lower vigor and poorer height growth, whereas the independent analysis of an earlier section failed to disclose a significant difference in the height growth achieved by balsam fir and spruce seedlings either under suppression or following release. One must conclude,

TABLE 4. Apparent trends of balsam fir content in forest succession: plots A-1 to 7, Laniel; B-1 to 12, Black Sturgeon; C-1 to 6, Cedar Lake.

Plot	Trees/acre: 1950 Fb	Sw & Sb	RATIO Fb:S	Sdlgs./acre: 1950 Fb	Sw & Sb	RATIO Fb:S	TREND OF Fb Sdlgs.'50 cf. Trees	Sdlgs./acre: 1955 Fb	Sw & Sb	RATIO Fb:S	TREND OF Fb Sdlgs.'55 cf. Sdlgs.'50
A-1	1038	67	15:1	9880	320	31:1	INCREASING	7150	190	38:1	INCREASING
A-2	1750	43	41:1	2020	70	29:1	INCREASING	3490	110	33:1	INCREASING
A-3	568	158	4:1	3250	950	3:1	DECREASING	2630	620	4:1	INCREASING
A-4	308	11	28:1	740	120	6:1	DECREASING	330	25	13:1	INCREASING
A-5	919	69	13:1	480	370	1.3:1	DECREASING	300	25	12:1	INCREASING
A-6	510	8	64:1	1180	50	24:1	DECREASING	220	none	All Fb	INCREASING
A-7	782	13	60:1	4660	190	25:1	DECREASING	2800	100	28:1	INCREASING
B-1	39	8	5:1	11440	480	24:1	INCREASING	6630	320	21:1	DECREASING
B-2	268	84	3:1	9370	350	27:1	INCREASING	5650	210	27:1	NO CHANGE
B-3	226	257	0.9:1	10910	280	39:1	INCREASING	7370	200	37:1	DECREASING
B-4	377	47	8:1	11240	840	13:1	INCREASING	6160	520	12:1	DECREASING
B-5 (A-B)	436	18	24:1	13340	160	83:1	INCREASING	6210	110	56:1	DECREASING
B-5 (I-T)	478	18	26:1	14970	130	120:1	INCREASING	8960	80	112:1	DECREASING
B-6	512	99	5:1	3380	50	67:1	INCREASING	2880	40	71:1	INCREASING
B-7	377	235	2:1	10820	370	29:1	INCREASING	7200	280	26:1	DECREASING
B-8	406	92	4:1	5670	490	12:1	INCREASING	3790	290	13:1	INCREASING
B-9	229	197	2:1	8740	580	17:1	INCREASING	7520	580	14:1	DECREASING
B-10	736	28	26:1	13770	200	69:1	INCREASING	7810	110	71:1	INCREASING
B-11	720	250	3:1	5250	25	210:1	INCREASING	3680	25	147:1	DECREASING
B-12	807	42	19:1	320	none	All Fb	INCREASING	280	none	All Fb	NO CHANGE
C-1	685	41	17:1	3220	360	9:1	DECREASING	-- PLOT DESTROYED BY ROAD CONSTRUCTION ---			
C-2	279	67	4:1	2330	110	21:1	INCREASING	2220	190	12:1	DECREASING
C-3	293	110	3:1	4390	500	9:1	INCREASING	2700	380	7:1	DECREASING
C-4	138	183	0.8:1	7710	2650	3:1	INCREASING	5280	1390	4:1	INCREASING
C-5	385	229	2:1	2890	390	7:1	INCREASING	2300	430	5:1	DECREASING
C-6	525	13	40:1	6280	310	20:1	DECREASING	4760	340	13:1	DECREASING

2 x 3 contingency test for regional independence of apparent trends of 1950 seedling tallies compared to original stands.

	LANIEL	BLACK STURGEON	CEDAR LAKE	
INCREASING	1 (4.85) X^2 = 3.06	13 (9.00) X^2 = 1.78	4 (4.15) X^2 = 0.00	18
DECREASING	6 (2.15) X^2 = 6.90	0 (4.00) X^2 = 4.00	2 (1.85) X^2 = 0.01	8
	7	13	6	26

TOTAL CHI-SQUARE = 15.75
2 d. of f.
p = <.001

2 x 3 contingency test for regional independence of apparent trends of 1955 seedling tallies compared to 1950 seedling tallies.

	LANIEL	BLACK STURGEON	CEDAR LAKE	
INCREASING	7 (3.35) X^2 = 3.98	3 (5.25) X^2 = 0.97	1 (2.40) X^2 = 0.82	11
DECREASING	0 (3.65) X^2 = 3.65	8 (5.75) X^2 = 0.88	4 (2.60) X^2 = 0.75	12
	7	11	5	23

TOTAL CHI-SQUARE = 11.05
2 d. of f.
p = .004

therefore, that the available evidence points to the ecological equivalence of established spruce and balsam fir seedlings.

There is some evidence in the present data to suggest that these ratios are being influenced by differential establishment of new seedlings following devastation. A comparison of the seedlings per acre data

in 1950 and 1955 for plot A-2 will disclose that during this interval there was an increase in the number of both balsam fir and spruce seedlings, while on plot A-3 there was an increase in the number of balsam fir seedlings alone. Reference to the continued establishment of seedlings on these plots has already been made in an earlier section of this paper. On plot B-9 at Black Sturgeon Lake, and on plots C-2, C-5 and C-6 at Cedar Lake, there was a slight increase in the number of spruce seedlings, while there was a decrease in balsam fir seedlings throughout the plots at Black Sturgeon and Cedar lakes. These latter observations suggest that the patchy and generally lower mortality of spruce trees following budworm devastation may occasionally provide a continuing seed supply for spruce regeneration after the balsam fir overstory has been eliminated. At Cedar Lake, where three of the five plots measured in 1955 show an increase in numbers of spruce seedlings, the greater proportion of black spruce in the overstory is clearly a relevant factor in the problem, since black spruce is relatively immune to budworm damage. It is concluded that, while no good evidence exists to support a hypothesis of a difference in survival of spruce and balsam fir seedlings, there is some evidence to suggest that a differential establishment of new seedlings may bring about minor changes in the ratio of spruce and balsam fir seedlings following a budworm outbreak.

A comparison of the 1955 regeneration retally with the original tree tally. This comparison has not been set out explicitly in Table 4, since with a few minor changes in the Laniel data it is a repetition of the comparison of the 1950 seedling tally to the original stand. Changes in seedling abundance at Black Sturgeon and Cedar lakes during the five-year interval between tallies failed to alter any of the trends of the 1950 regeneration in relation to the original stand, although it is unfortunately impossible to confirm this observation for plot C-1 at Cedar Lake. At Laniel, the ratio of fir to spruce on plot A-3 has returned to exactly that observed in the original stand, so that this would be given the notation *no change*. No spruce seedlings were tallied in 1955 on plot A-6, where an estimate of 50 spruce seedlings per acre was obtained in 1950, so that on this plot the trend measured by the 1950 tally appears to have been reversed. In this connection it must be appreciated that an estimate of 50 seedlings per acre, based on a 10 percent sample, represents an actual tally of only five seedlings on a one acre plot, or, in this instance, a tally of eight seedlings on a 1.6 acre plot. During this same five-year interval, 154 of the 189 balsam fir seedlings originally encountered on this plot were also destroyed, so that the possibility remains that this apparent reversal of the earlier trend may be a small-sample effect, and that spruce may still exist on the remaining 90 percent of the plot in much the same proportion as it did in 1950. These anomalies will be clarified by future re-examinations of the plots, which, it is hoped, may be conducted as 100 percent tallies of young trees of measurable diameter.

Although changes in seedling abundance during the interval between tallies have made only these minor differences in the original trends, there is still some evidence of an overall pattern to the changes that have taken place. If the observed frequencies in the two contingency tables at the bottom of Table 4 are themselves compared, there is an evident tendency for the one to be a mirror image of the other: at Laniel, where six of the seven plots showed a decrease in balsam fir in 1950, all seven of the plots in 1955 show the opposite trend, so that the area as a whole is tending to return to a level closer to that of the original stands. At Black Sturgeon and Cedar lakes the same applies in the opposite sense: where there was a tendency towards an increase in balsam fir in 1950 there is a general improvement in the proportion of spruce in 1955, granted that in no instance

has the trend measured in 1950 in relation to the original stand been altered by these changes. In relation to the life cycles of a succession of forest stands, the tally of a seedling population in a particular year is equivalent to arresting a fluctuating process at a moment in time when it may be expected to depart by some considerable degree from its modal position. While the question is still one for speculation, the work of Blais (1954) has shown that the spruce budworm has long been active in the harvesting of mature stands of balsam fir even without human alteration of the forest composition, and there would seem to be no particular point more favorable than any other in the interval between the last glaciation and the present time that one might choose as the point of initiation of this process. The same may certainly be said for periodic devastation by fire, which, in setting back forest succession to a more pioneer stage than does budworm devastation, may possibly provide from time to time a more satisfactory seed bed for the establishment of spruce seedlings. But one should be critical from the first of any theory of the proportionate increase of one tree species over another, which, if it had been uniformly operative following every major forest disturbance, would surely have long since completely eliminated the less favored species.

Conclusions

The most important conclusion pointed up by the present study is that whatever the trends that may develop following budworm devastation, these trends appear to do so on a regional basis. There is, then, every reason to suppose that the various conflicting theories on the role of the spruce budworm in forest succession have each been based on sound observation, but observation restricted in each instance to a limited forest region. Under the influence of a locally favorable site and climate it is evidently possible for either spruce or balsam fir to increase in proportion following budworm devastation, but there is no evidence in the present study to support the contention that either possesses inherently greater competitive abilities under all circumstances. The conclusions of this study suggest that the problem should be reopened on a regional basis wherever fir, spruce, and the spruce budworm are prominent features of the forest complex.

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Summary

1. For many years there have been differences of opinion on the role of the spruce budworm in forest succession. Interest has centered in recent years on the theory that the proportion of fir in mixed balsam fir-spruce stands tended to increase following budworm outbreaks. An earlier theory suggested that the spruce budworm, which shows a marked preference for balsam fir as a host tree, might actually tend to increase the proportion of spruce in succeeding stands.
2. Data are presented on forest succession and related problems from studies conducted in budworm devastated stands in northwestern Quebec, and in northcentral and northwestern Ontario.
3. Data gathered during these studies afforded the opportunity to confirm Turner's (1952) conclusion that mortality of balsam fir following budworm devastation is correlated with the percentage of total basal area con-

tributed by the balsam fir component of the stand.

4. Evidence was obtained of a curvilinear progression in the frequency of occurrence of successively less abundant shrub species which have come to dominate many of the devastated study areas.
5. Balsam fir and spruce seedlings were found to have similar frequency distributions by height classes, both immediately after budworm devastation and after five years of released growth. This observation indicates that there is no appreciable difference between balsam fir and spruce in either their shade tolerance or their ability to profit from release.
6. A decrease in balsam fir seedling numbers of between 20 and 65 percent was observed between the regeneration tallies conducted in 1950 and in 1955. Correlation analysis indicated that approximately 72 percent of this decrease could be attributed to coverage by wind-broken, budworm-killed trees. A further 16 percent of the decrease appeared attributable to severe competition from shrub growth, although it is probable that this latter percentage is not totally independent of that already attributed to coverage by broken trees.
7. Trends in forest succession, as indicated by comparisons of the ratios of balsam fir to spruce in the original stands and in the seedling populations, proved to be strongly dependent upon the region in which the data were gathered. Data from northwestern Quebec indicated a general increase in the proportion of spruce, while data from north-central Ontario showed a consistent increase in proportion of balsam fir. Data from northwestern Ontario suggested a slight increase in fir, but the evidence was not conclusive.
8. Comparison of the fir-spruce ratios measured by the 1950 and 1955 seedling tallies indicated no general trend towards an increase in either spruce or fir during this period. Changes that did occur were again regionally dependent, but on only one of the 26 study plots was the change sufficiently great to reverse the trend already indicated by comparison of the 1950 tally with the original stand.
9. What evidence there is suggests that established balsam fir and spruce seedlings are more remarkable for their ecological equivalence than for any differences in ability to survive under competition that can be detected in the data presented. There is some evidence to suggest that differential establishment of new seedlings, particularly spruce seedlings, may bring about minor changes in the spruce-balsam fir ratio after a budworm outbreak.
10. It is suggested that the apparent regional dependence of trends in forest succession following devastation has been at least partly responsible for the widely divergent theories on the role of the spruce budworm in forest succession. The present study indicates that the problem is not one which lends itself to a generalized answer independent of the particular forest region under consideration.

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